

2.1.2 Identification Of Gamodemes In Populations -

The analysis of population structure has been hampered by the absence of tools to identify breeding units. Unless the members of populations were identifiable by striking visible or similar appearances, a subdivided local population would remain completely undetected. Workers generally were forced to assume homogeneity in natural populations even though detailed studies invariably indicated the presence of heterogeneity.

We have almost completed the reprogramming of analyses developed by Makela (1975) and Makela and Richardson (1977) to make them more easily used, better documented and probably more reliable. Since the data input format differs from earlier versions, we have delayed the completion of the analyses of the last year study in Hawaii until now. In addition, Dr. Peter Smouse, University of Michigan, and I have been developing a multivariate analysis of mixed gamodemes, which will be very useful in the complete analysis of such data (see Appendix C for draft of the manuscript). Therefore, the analysis of Hawaiian Drosophila, particularly D. mimica, is reaching a point where the results soon will be summarized for publication.

The results for 1974 and 1976 indicate that at least two gamodemes are identifiable in Bird Park, and their proportions change. In an earlier study a single homozygote of APH declined during a period of very acid rainfall during a volcanic eruption, but the original proportions of "genotypes" in the population returned quickly (Rockwood, 1969). We earlier postulated that the recovery might have reflected migration into the affected population from a population in a protected area receiving less rainfall (Richardson and Johnston, 1975), rather than selection against this particular electromorph. However, the most probable explanation is neither selection on this particular locus nor migration, but that the locus is a marker which distinguishes between two gamodemes. One gamodeme may have been more severely depressed by the adverse conditions during volcanic eruption, but recovered rapidly after the eruption ceased, or, alternatively, the fluctuation represented normal seasonal fluctuations of separate populations. Consistent with this latter interpretation is the recently published result of similar allozymic fluctuations in the absence of an eruption (Steiner, 1979).

2.2 Screwworms

The idea of eradication of a species by the release of large numbers of males sterilized by massive doses of X-rays was conceived about 25 years ago by Dr. E. F. Knippling and developed by him, Dr. R. C. Bushland, and their colleagues. The screwworm has been successfully eliminated from several Caribbean islands and from the southeastern United States. A "barrier zone" along the U.S.-Mexico border was established in 1964, with the intent of preventing a re-invasion of the United States each spring by the populations surviving below the freeze line. This barrier zone was effective for several years, but effectiveness in the last decade or so has been erratic.

In a recent symposium (Richardson 1978) we sketched a number of areas in which genetic and ecological processes could be factors contributing to the difficulties experienced by the "eradication" program. From our perspective outside the USDA program, it appeared that this massive effort in pest control had initiated a very interesting experiment from which we could learn many features about the responses of a community placed under intense stress. Our suspicions were that the pest was comprised of one or a few component species that would be differentially stressed, depending on their relationship to the population being released (Makela and Richardson, 1979). Indeed, we have discovered that this suspicion was substantially correct.

The results of the genetic analyses during the past year may be summarized briefly. There are many cryptic gamodemes (and presumably are different species or semi-species), many of which are sympatric. We have identified at least 7 such groups in the United States last year, 3 of which were found below the freeze line last winter in Mexico, and the others are yet to be found again this year. All of these were collected while up to 3000 sterile flies were being released per square mile per week, and control was limited to population suppression rather than eradication. The released flies were of a different type than any of those identified, however. While some of the types have been found only above the freeze line, their method of surviving freezing temperatures is unknown. Diapause or other adaptive responses not previously associated with the genus may be involved. We have found several additional species in Mexico which have not been found in the United States.

The genetic techniques used to distinguish the cryptic species involve chromosome karyotypes derived from quinacrine-stained metaphase chromosomes (developed and performed by Dr. John Ellison) followed by electrophoretic analyses of the same larvae from which the chromosome preparations are prepared. The collections of larvae typically are obtained from naturally infested wounds in livestock (collected by or under the guidance of Dr. W. W. Averhoff). The karyotypes occur in distinct groups, differing by heterochromatin concentrations (primarily on sex chromosomes) and chromosome morphology. We have not found types precisely the same as those with karyotypes published before the construction of the barrier zone. Thus, it appears that either these types have, indeed, been eradicated and now are extinct, or else they have been suppressed and/or their geographic range has been reduced such that our sampling has failed to reveal their presence. Concordant with the chromosome groups are sets of some allozyme electromorphs unique to some karyotypic groups, while there are strong differences in frequencies in other cases. In one instance a pair of sympatric groups are distinguishable only by allozyme assay.

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We have found examples suggesting strong differences in host preferences, even between such similar hosts as cattle and sheep. Niche separation in this way closely parallels the plant substrate preferences in Drosophila we have studied previously. Also similar to Drosophila we have studied, there is accumulating evidence that some species oviposit less than a dozen eggs in a clutch in some individual hosts, while others are more likely to deposit up to about 50 eggs, and a few typically deposit up to 200 eggs. In the latter case and in some of the intermediate cases they also will re-oviposit on previously infested wounds, whereas in some cases there is only one oviposition per wound. Clearly these species represent a wide range of reproductive strategies, from "r-selected" to "K-selected" species.

As will be addressed in the section below, this extreme diversity of reproductive strategies between closely related, sympatric species is intriguing. As in Drosophila, such diversity of screwworms is very difficult to discover by casual observation of individuals. In Drosophila we commonly discover the existence of some of the cryptic species when we attempt to culture certain types. Since the K-selected species often have specialized cues for oviposition, and often lay only a few eggs, culturing in the laboratory is a challenge. When we have a "single species" which is easily cultured, but then find certain lines are very difficult to culture, we have learned to take this anomaly as a strong clue of the presence of a cryptic K-selected sibling species. Such anomalies will likely be important in future studies, whether they involve Drosophila, screwworms, or other taxa.

The geographic ranges of the cryptic species of screwworms also are highly variable. Some extend over a thousand miles. One type is found from Mazatlan to Phoenix, while another sometimes extends between San Antonio and El Paso and south from San Angelo across "west Texas," presumably into the Chihuahuan Desert. Still others have only been found in a single locality, such as north of Tampico within 175 miles of the Gulf of Mexico and with a north-south range of about 200 miles. A few have only been found in a single collection, which may suggest either a restricted range, that or they occur in very low frequencies, causing difficulty in sampling.

Although only historical speculations may be made at the present time, it is plausible that the initial successes of the eradication program represented the extreme suppression, or possible extinction, of a dominant species in Florida and Texas, with subsequent outbreaks representing the increase of previously secondary species. As the sterile males to be released in the future are matched to specific species, we will be able to observe changes in the relative proportions of the remaining species. Thereby "species releases" (significant and permanent expansion in numbers or the range of a natural population) for secondary species will be monitored. Also, it is likely that we will relate some of these census and geographic changes of the species to weather and other variations occurring over a few years. These factors may demonstrate some characteristics besides competition or interference by related species which have restricted the species ranges or retarded their seasonal increase.

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With the theoretical studies proposed for this contract in the next period, we hope to gain some insight into the community dynamics ("species release" of secondary species, as various numerically dominant ones are eliminated or suppressed, for example) and develop appropriate models for the type of responses precipitated by an autocidal biological control program or any other selective reduction in the Malthusian parameter for the intrinsic rate of population increase. In addition, responses of other members of a community and the resulting effects on stability of the community will be brought into focus by the models.

2.3 Ticks

The research on ticks has been supported by the USDA during the past year (while this Contract with DOE has supported the research on Drosophila and screwworms). However, for completeness of the unpublished background data as it relates to our plans for the next contract period with DOE, a brief review of this work will be given.

Ticks represent a different type of experimental material to either screwworms or Hawaiian Drosophila, having received a concerted effort over the past several decades to reduce the population by chemical insecticides. In some cases, eradication of particular species by insecticide treatments over large areas has been attempted. (They are vectors for a number of diseases of livestock and humans.) Our work has centered on those which have received persistent treatments of various insecticides for a number of years. In certain cases species have managed to extend their ranges greatly in the face of such stresses as the insecticide treatments. Clearly the community has been altered, likely by human activities, but not necessarily to the detriment of the pest species. We are now interested in identifying the reproductively isolated populations (gamodemes, which in many instances probably represent cryptic species). From this base line we hope to gain some insights relating the range extensions to the factors responsible for range extensions, whether they be reflections of genetic changes in the population, or other factors having a closer connection to environmental modifications by man. The understanding of community instability, whether reflecting changes involving local or absolute extinction, or greater packing of a local community by the range extension into a new area, represents the broad objective of this research.

In collaboration with USDA researchers (coordinated by LaWanda Hunt) we have identified several cases of presumptive cryptic species in three presently recognized species of ticks. We are now in the process of identifying the ranges of each gamodeme, as well as conducting various breeding tests among the several populations we have found.

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Dynamics and Stability

of

Phyletically Packed Communities

September 12, 1979

Renewal Proposal, DOE Contract

DE-AC05-79ET01834

Departments of Zoology and Physics

University of Texas at Austin

R. H. Richardson and Jack S. Turner

with assistance of

Dan Vasco

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1.0 PERSPECTIVE

This project in recent years has been oriented toward field studies of Hawaiian Drosophila (habitat selection, dispersal, population structure, and "phyletic species packing"). Last year the techniques used for the studies in Hawaii were applied to the analysis of two groups of pests, "screwworms" and ticks, which represented highly disturbed populations -- the former by the species-specific technique of sterile male releases, and the latter by the non-specific technique of insecticide applications. Although there remain a number of "loose ends" to tie up the field studies conducted under this contract, particularly the completion of data analyses and publication of results, a better theoretical foundation is clearly needed for future studies of the evolutionary processes involved in rapidly evolving communities. Communities which have been disturbed by man's activities, or which are being re-established after a disturbance are examples of such rapidly evolving communities.

Several biological aspects need to be parameterized to guide measurements to be made in actual situations. Also some idea of the relative importance of the several parameters is needed for establishing the priorities in planning and implementing more field studies. "Importance" is determined for practical purposes by two features: (1) estimability of parameters and (2) impact on the system when parameters values change. Evaluating both of these factors depends upon the availability of an adequate theoretical model for the community, which at the present does not exist. In particular, recent findings all indicate that there are complexities in community composition (sympatric cryptic species or subspecies), and measurements of community responses disregarding this feature may be highly unreliable. For example, apparent large effects may reflect only a numerical change in one dominant component of several species, while, alternatively, dramatic extinctions of secondary species might be missed altogether.

The development of partial to extensive reproductive isolation is now known to have developed in nature in some organisms in a matter of a few decades, and such complexes of related types may develop in time spans relevant to studies of disturbed populations (with the extreme case being phyletic species packing (Richardson, 1974; Richardson and Smouse, 1976)). Synthesis of populations having considerable degrees of reproductive isolation also has been achieved in laboratory studies spanning only 15-20 generations. While Templeton (in press, and personal communication) has identified sufficient genetic conditions to allow such rapid progress through the speciation process, at present we have almost no theoretical benchmarks and parameterization for measuring and studying the statics and dynamics of such rapidly evolving populations and communities.

Funding of this contract will allow an effort to be directed toward building certain models which we can use for characterizing these systems. This effort will be conducted in collaboration with Dr. Jack Turner, who will be a Co-Principal Investigator while we focus on theoretical developments. Dan Vasco, a graduate student who has pursued a double major in Zoology and Mathematics, will actively participate in this work. Dr. Turner has followed this project for several years,

motivated by his general interest, while his research during this time has been dynamic model building for a number of non-equilibrium chemical systems. He is a faculty member in the Physics Department and a staff scientist for the Center for Statistical Mechanics and Thermodynamics (headed by Professor and Nobel Laureate Ilya Prigogine). Dr. Peter Allen is also a member of this group. Although his principal academic residence is in the Brussels lab of Ilya Prigogine, he is a frequent visitor to Austin, and will be a peripheral contributor to the modeling effort planned.

2.0 PROGRESS REPORT (OCTOBER 1976 TO SEPTEMBER 1979)

2.1 Drosophila

2.1.1 The Role Of Dispersal (with J. S. Johnston, Tex. A&M Univ.) -

Gene flow has been considered to be a significant limiting factor to genetic differentiation of populations of a species. Although some evidence suggests that this factor may not be as strong as initially thought (Ehrlich and Raven, 1965; Endler, 1973, 1977), the bulk of the opinion in the literature remains unchanged.

Evidence that extensive differentiation has evolved without disjunct populations can be found in numerous field studies (see reviews by Jain and Bradshaw, 1966; Ehrlich and Raven, 1965; Antonovics, et al., 1971). Experiments of numerous workers (Thoday and Gibson, 1962, 1970; Dobzhansky, 1971; Endler, 1977) show that marked differentiation may evolve quickly in spite of high levels of gene flow. Although theoretical investigations (Endler, 1973, 1977; May et al., 1975; Slatkin, 1978) argue that geographical differentiation is required to initiate the process of speciation, allopatry per se may not be a prerequisite for speciation, but rather, habitat selection in a spatially heterogeneous environment may be functionally equivalent.

Templeton (1978) showed that environmental variation is important only for "coarse grained" habitat, when the species spends the majority of its time in one or another selected habitat. This mathematically derived observation has great intuitive appeal. It says that a heterogeneous environment produces increased variance only when the organism recognizes the heterogeneity and spends a disproportionate amount of its time and reproductive effort in a selected habitat. In other words, an increase in genetic heterogeneity in a fine grained environment depends upon habitat selection.

To date, habitat selection in Drosophila has been shown in D. pseudoobscura (Taylor and Powell, 1977), in D. mimica (Richardson and Johnston, 1975), and in D. affinis and related species (Richmond, 1978). These studies helped to destroy a long-standing belief that Drosophila move randomly throughout an area (Johnston and Heed, 1976; Richardson, 1974; Richardson and Johnston, 1975) and focused attention on the potential for habitat selection and microhabitat differentiation in species which are capable of relatively long-range movement.

Recent theoretical studies have focused upon the role of both selection and dispersal in the maintenance of spatial heterogeneity in gene frequencies. The results are sometimes conflicting. Endler (1973) and May et al. (1975) concluded that gene flow is ineffective against a selective gradient, while Karlin and Richter-Dyn (1976) and Slatkin (1978) conclude the contrary. In 1977 Endler (p. 47) stated that "there appears to be an intermediate optimal level of gene flow at which a real differentiation is greatest; at intermediate gene flow levels a combination of patch size and patch value is at a maximum." Slatkin (1978), studying spacial variation in polygenic characters, found that the width of a cline will be approximately the "characteristic length" of the species, where characteristic length is a simple function of the average dispersal length, $\bar{l}$, and a spacial variable, E : $l_c = \bar{l} E^{-1}$, where l_c is characteristic length, $\bar{l}$ is average dispersal distance and E is a spacial variable. Further, he concludes that dispersal can increase the spacial variance in gene frequency, producing a steeper cline than would be produced with the identical spacial heterogeneity but no dispersal.

In our study of dispersal and habitat selection in Hawaiian Drosophila, the vegetation has been described by species and abundance at 5 levels for every 4-meter square in study areas in two kipukas. Multiple stepwise regression shows a highly significant relationship between the vegetation and the flies. Four plant species account for 56% of the variation in D. mimica in each 4-meter plot. Similarly, 5 plant species account for 58% of the variation in D. imparisetae, 3 plant species account for 66% of the variation in the melanogaster group, and 2 plant species account for 36% of the variation in D. immigrans. The majority of the variation in the two endemic species, D. mimica and D. imparisetae, are accounted for by indigenous and endemic vegetation. The distribution of the exotic Drosophila are accounted for by exotic plant invasions.

These results suggest that, given an evolving community such as that represented by endemic species of flies and plants, the introductions of exotic species of either flies or plants have caused minimal shifts of the original community structure (although the population sizes may have been adversely affected). The success of the invasion still is not certain, and monitoring changes over time henceforth will be possible using these results as references. The analysis of gamodeme complexity is underway in the endemic flies, but earlier results suggest that several gamodemes are present for each taxon. Their habitats are not yet known, so that the patterns of interactions cannot be determined. (It might also be noted that recent work of Eckstrand and Richardson (in manuscript) has revealed physiological differences among populations separated by only a few meters.)

In other studies, the role of air movements on dispersal has been shown for several species (Appendix A) and habitat selection has been shown to play a critical role in niche isolation of two closely related species (Appendix B).

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2.3 Ticks

The research on ticks has been supported by the USDA during the past year (while this Contract with DOE has supported the research on Drosophila and screwworms). However, for completeness of the unpublished background data as it relates to our plans for the next contract period with DOE, a brief review of this work will be given.

Ticks represent a different type of experimental material to either screwworms or Hawaiian Drosophila, having received a concerted effort over the past several decades to reduce the population by chemical insecticides. In some cases, eradication of particular species by insecticide treatments over large areas has been attempted. (They are vectors for a number of diseases of livestock and humans.) Our work has centered on those which have received persistent treatments of various insecticides for a number of years. In certain cases species have managed to extend their ranges greatly in the face of such stresses as the insecticide treatments. Clearly the community has been altered, likely by human activities, but not necessarily to the detriment of the pest species. We are now interested in identifying the reproductively isolated populations (gamodemes, which in many instances probably represent cryptic species). From this base line we hope to gain some insights relating the range extensions to the factors responsible for range extensions, whether they be reflections of genetic changes in the population, or other factors having a closer connection to environmental modifications by man. The understanding of community instability, whether reflecting changes involving local or absolute extinction, or greater packing of a local community by the range extension into a new area, represents the broad objective of this research.

In collaboration with USDA researchers (coordinated by LaWanda Hunt) we have identified several cases of presumptive cryptic species in three presently recognized species of ticks. We are now in the process of identifying the ranges of each gamodeme, as well as conducting various breeding tests among the several populations we have found.

2.4 Recent Publications Derived From This Contract

1. Book: The Screwworm Problem, Evolution of Resistance to Biological Control. R. H. Richardson, ed. Univ. Texas Press. 151pp. (1978)
2. Richardson, R. H., Peter E. Smouse and Martha E. Richardson. 1977. Patterns of molecular variation. II. Associations of electrophoretic mobility and larval substrate within species of the Drosophila mulleri complex. Genetics 85:141-154.
3. R. H. Richardson and W. W. Averhoff. 1978. A cattleman's view of beef production with and without screwworms. In The Screwworm Problem, R. H. Richardson, ed. Univ. Texas Press. pp.3-9.
4. Makela, Merry Eve and R. H. Richardson. 1978. Hidden, reproductively isolated populations: One of Nature's countermeasures to genetic pest control. In The Screwworm Problem, R. H. Richardson, ed. Univ. Texas Press. pp.49-66.
5. J. Spencer Johnston. 1978. Dispersal behavior and biological control of insects. In The Screwworm Problem, R. H. Richardson, ed. Univ. Texas Press. pp.113-127.
6. J. Spencer Johnston. A new cactiphilic Drosophila niche: An analysis of the behavior and ecology of two desert-adapted Drosophila. (in manuscript, see Appendix A).
7. J. Spencer Johnston. Selection for anemotaxis (wind directed movement) in laboratory and wild caught populations of Drosophila. (in manuscript, see Appendix B).
8. Peter E. Smouse and R. H. Richardson. Genetic cluster analysis of sibling gamodemes. (in manuscript, see Appendix C).

3.0 RESEARCH PLANS

3.1 Rationale

3.1.1 Phyletic Species Packing -

Community Stability, Background -- From computer simulation studies Robert May and others have found that randomly constructed "alpha matrices" or communities show no relationship between complexity or species diversity and stability. However, Larry Lawlor (1978) showed that these studies had an infinitesimal chance of finding the stable communities. The biological reality is not addressed by "randomly" constructed communities. Communities which actually will form are a special subset of all possible communities, and the real question lies in the density of stable communities within this realistic subset of possibilities. However, Lawlor does not approach the question of how one

identifies the realistic subset of possibilities, nor how this subset originates in the first place. One approach, however, is suggested by phyletic species packing, which certainly would produce alpha matrices with large interdependencies among diagonal and off-diagonal elements. Such relationships may lead to connectance and stability in the system. It is worth noting that our work in cytogenetic and molecular rates of evolution indicate that the time required to evolve such a community in nature may not be as long as we traditionally have assumed.

Furthermore, Templeton (in press and personal communication) has developed predictive models delineating genetic circumstances whereby rapid speciation is to be expected. These circumstances are precisely met in screwworms, ticks, and a host of other pest taxa which are exposed to periodic bottlenecks from transportation to new areas or by sporadic widespread suppression by pest control measures. They are genetically heterozygous, producing a mass of variability, derived from a few surviving individuals, which subsequently is released by population buildup with a genetic system having extensive recombination (viz. numerous chromosomes). In addition, such features might be an important consideration in selecting components for re-establishing a community in a denuded area where a rapid approach to stability would be desired.

We are addressing two theoretical questions: one concerns the evolution of stable communities, while the other concerns the stability of communities whose mathematical structure is changed by the addition or removal of species. In the first case, we hope to better understand the conditions whereby a stable community evolves. How can the stability increase, or even develop from an originally unstable community without serious extinction or other undesirable effects? This condition might be significant for the re-establishment of a community after a major disturbance. Our objective might be viewed as establishing a new community which would "crystallize" rapidly in a desirable way.

In the other case, we focus on how the community stability is affected by the removal or addition of members within a cluster of related species. In this case, we are less interested in the circumstances whereby a community experiences significant local extinction as a result of an unstable condition, but we are concerned with circumstances where the abundances of several taxonomic components shift drastically. It may be this type of adjustment that causes some species to extend their range, or become pests in response to an environmental disturbance. This process of "species release," particularly among invertebrates, may present a greater potential cost to society than the more conspicuous changes of "endangered species." Shoreline pollution, for example, is the cause of several serious upsets, the full impact of which are not yet known. We know of several cases of marine invertebrates having cryptic gamodemes much like the insects of this study. Such complex "species" may be more likely to produce a new pest than "species" with single gamodemes.

Community Stability, Evolution -- If a diverse community evolves from a few founder species, it will consist of clusters of related species (or gamodemes). These will be very similar in many ways, and there will be a high genetic correlation among the members of a cluster.

In plants, this process has been studied for parapatric populations, where populations were established on dumping sites of old silver, lead or copper mines (e.g. Antonovics 1968; McNeilly 1968; Antonovics and McNeilly 1968). In animals, Thoday and Boam (1959) reported genetic divergence by disruptive selection in Drosophila without sexual isolation, and then found evidence for the origin of isolation (Thoday and Gibson 1962). However, our work on Drosophila is the first from natural populations to our knowledge that parallels the laboratory work of Thoday and his associates, and our Drosophila results closely parallel some of those with plants. The main difference between the plants and insects lies in the spatial distribution of individuals -- plants are held in place, and the divergence is between parapatric populations, while the insects are mobile and the gamodemes often are sympatric. One should keep in mind that the distinction may be more apparent than real where habitat selection is strong.

From the biological point of view, a community evolving by a process of speciation has certain features not found in one evolving by colonization. Component species may co-evolve rapidly, thereby developing a particular pattern of competitive interactions. These interactions are at the heart of the evolutionary process of community stability, and will largely determine the type of responses by the community to environmental disturbances.

Consider the following possible features, which were suggested in part by our understanding and "best guesses" of the features found in the Drosophila cases in Hawaii and the desert breeding species of the D. longicornis sibling cluster. Gamodemes derived recently from a common gene pool will share most of the highly organized genetic systems, and consequently will generally be adapted to similar macro- environmental conditions. They will generally be sympatric, and will be exposed to the same general conditions. These gene complexes thereby may be preserved by the same selection forces. However, often these macro- environmental features are extrinsic (e.g., not consumed) so that competition will not exist between the related gamodemes on these axes of the niche hypervolume. In other cases the limitations of resources will be infrequent or mild, thereby producing only gentle competition. Should severe competition (very limited resources) potentially be present for any axis of the niche hypervolume, however, a single gamodeme may experience serious depression (e.g., famine) with no significant genetic response, or a diversity of niches with some correlations among the axes may allow the maintenance of a polymorphism with a high genetic load. However, upon the development of reproductive isolation between any subpopulations representing differently adapted forms (morphs of the polymorphism), selection then can act to diverge the subpopulations, forming different gamodemes with different gene frequencies.

Recalling the extreme diversity of r- and K-selected species often found among a cryptic series of sympatric taxa, we may imagine one way that a generalist may be evolutionarily unstable. Often eggs are deposited in clutches, or in a short time when the substrate reaches a certain condition. If there are genetic differences for, say developmental rate in larval stages, which often is correlated with nutritional level and fecundity as well, then those types developing slower will not have an opportunity for the males to mate with females

of the more rapidly developing types. The faster developing females would have been mated by the time the more slowly developing males eclosed and reached maturity. Dispersal behavior can indirectly be affected by hormone dynamics. If the faster developing males has also tended to disperse, then we have a system of positive assortative mating derived from the differences in developmental rate.

The conditions for sympatric speciation (or population subdivision with limited gene flow among component parts) have been examined theoretically by Maynard-Smith (1966), where he has shown that speciation is possible. We wish to examine this process at the level of co-evolution of the gamodemes, where the niche space for the different gamodemes is exploited by the production of a series of "specialists" from a single "generalist" gamodeme, minimizing competition while maximizing effective utilization of resources.

One can make several predictions concerning the features of such clusters of gamodemes where members of each cluster are derived from an ancestral gene pool. For example, drastic changes in the environment may destroy an entire cluster at the same time. However, the chances of surviving a catastrophic change are improved by the subdivision of the ancestral gamodeme and genetic divergence among the derived gamodemes. This may happen in two ways. First, a cluster may form by spatial or temporal isolation as was studied long ago by Wright (1932). He noted this was a population structure that allowed rapid evolution, but without speciation beforehand. (As noted in Section 2.1, actual spatial or temporal separation need not be extreme for diversity to develop.) Second, a cluster may form by speciation as predicted by Templeton's work, which could produce community diversity in situ. In either case the total genetic variance in the ancestral gene pool is increased by subdivision and genetic divergence, allowing more rapid responses to selective forces.

Although the magnitude of increase in genetic variance depends on the pattern of divergence and the nature of the genetic system, even with random divergence we know that the subdivision of a gene pool into inbred lines doubles the additive genetic variance. Templeton shows how some cases result in a genetic transilience and extensive diversity is expressed while retaining genetic variance within populations. If at least one of the gamodemes survived the catastrophe, in time all destroyed gamodemes likely could be replaced. On the other hand, if the change were permanent, the competitive interfaces between the new clusters would show some features reminiscent of the old community.

With respect to the degree of resource utilization in total resource space, a more "tightly packed" community would be possible if it were formed by a series of specialists rather than fewer generalists. Beginning with generalists, we visualize rather broad niche spaces, with fairly low efficiency of resource use, particularly in the peripheral parts of the niche hyperspace. With increased specialization, those gamodemes selected for the peripheral areas would have more efficient resource utilization, and the same also would be possible at a later time as the gamodeme representing the mode of efficiency of the ancestral form were selected for a more confined niche space as the specialists formed in the periphery. The overall efficiency of resource

utilization would be expected to improve. Minor fluctuations in the environment may periodically destroy some of the specialist gamodemes, but regeneration of the community still could occur, the regenerated gamodeme coming from one of the related gamodemes still present. Therefore, in general, one would expect a community derived in this fashion to become more finely tuned to maximum resource utilization. An ancillary effect would be greater resistance to invasion of other species. There might be a moderate rate of turnover of the gamodemes, but with an overall reduced probability of total extinction of the cluster. This community would thereby evolve to increased "cluster" stability.

3.1.2 Related Theory And Historical Background -

3.1.2.1 Classical Population Genetic Models -

Two important theoretical results of population genetics can be related to changes in the fitness of genotypes in response to genetic changes and how their resulting evolution is effected: Fisher's fundamental theorem of natural selection (FTNS) and Wright's idea of adaptive topographies.

Fisher's FTNS has been rewritten in a more general form by Kimura (1958) as:

$$\frac{d\bar{m}}{dt} = V_g + \overline{\frac{dm}{dt}} + \overline{D \frac{d\phi}{dt}} \quad (1)$$

where $\bar{m}$ is the fitness parameter (averaged over genotypes), V_g is the genic variance, the second term is the average rate of change⁸ in fitness (of individual genotypes), and the third term measures the effect of gene interaction (D) and departure from Hardy-Weinberg ratios. In a constant environment with random mating only the first term remains and the theorem reduces to the form originally given by Fisher (1958). This equation implies that:

1. no evolution occurs unless genetic variance is present
2. the only part of genetic variance important in evolution is "additive"
3. the rate of evolution is dependent upon the genetic variance present
4. m is at a local maximum-- this relates to Wright's concept of an "adaptive topography"

5. at equilibrium, m is a constant, $m = r$ with the result that population growth is exponential according to

$$\frac{dN}{dt} = r N \quad (2)$$

Although these conclusions do not bear directly on our question of a population genetic mechanism for speciation, Fisher's FTNS does provide an intuitive idea of the nature of adaptive changes in a population. This is important in trying to obtain a concrete notion of the elusive concept of an organism's "fitness." Fisher's FTNS can be viewed in a quite general way. For example, one can argue that quantitative characters or traits such as clutch size, morphological characteristics, foraging strategies and behavioral mechanisms are related to "fitness" and, hence, are important in natural selection. Crow and Nagylaki (1976) showed, however, that such traits may not in general be optimized by natural selection. Nevertheless, Fisher's formulation provides a qualitative causal relationship between selection and the fitness of an organism in terms of the available genetic variability. In this same sense his result unites almost all the ideas of classical population genetics.

Wright's idea of an adaptive topography is easily illustrated using the equation:

$$\Delta p = p \frac{(1-p)}{2\bar{w}} \frac{\partial \bar{w}}{\partial p} \quad (3)$$

This equation establishes a connection between changes in the gene frequency, p , and the slope of the average fitness $\bar{w}$. Wright viewed $\bar{w}$ as an adaptive value that could be used as a "topographic map" plotted against gene frequencies; as $\bar{w}$ tends to increase, populations will move to the highest local point in this "adaptive topography" (Turner, 1968). Kimura (1958) restated this viewpoint as a maximum principle in the theory of natural selection. Recently, however, this viewpoint has been questioned (Shahashani, 1979; Edwards, 1977).

These pioneering ideas of Fisher and Wright have played an important role in nearly all general formulations made in classical population genetics. As far as making an actual contribution to our theoretical understanding of speciation and other radical genetic changes in population, very little has been done, and for this reason the generality of these theoretical results has been questioned (Mayr, 1978).

Much of the incentive for developing a theory of speciation has been provided by experimental and field studies. Although we do possess theoretical and experimental insights into the genetic basis of adaptation and speciation, a quantitative mathematical theory has been slow to emerge (Templeton, in manuscript). One model of speciation derived primarily from population genetics is based upon founder effects and the creation of genetic revolutions. Recently Templeton (op. cit.) formulated a predictive theory of the genetic conditions which are sufficient to produce a speciation event. Through a number of theoretical and experimental results, Templeton formulated a theory that predicts a rapid shift in the genetic environments which he labeled a "genetic transilience."

One interesting aspect of Templeton's theory is that he is able to distinguish speciation via the genetic transilience avenue from the classical avenue of gradual, adaptive, allopatric divergence. In some cases, such as in insect species that have undergone host shifts, the genetic transilience model predicts reproductive isolation without strict geographic isolation. When the external environment is changing radically, a population may undergo an extreme bottleneck, at least in local areas, so that a genetic transilience could occur. These conclusions are important in that, for the first time, a theory based upon extensive theoretical and empirical work (Templeton, 1974, 1979; Carson, 1975, 1979) has predicted that sympatric species may develop where ecological and genetic environments are changing rapidly.

3.1.2.2 Reformulation Of Classical Theories -

Virtually no theoretical work has been done in determining the ecological conditions that cause the genetic and ecological divergence of species, especially sympatric species. This probably results from the absence of ecological interactions in Fisher's and Wright's formulations of the classical theory. Recently, however, efforts have begun which are moving in this important direction. Of special significance is the theoretical work that developed from "evolutionary ecology." This viewpoint, started primarily by the late Robert MacArthur and Richard Levins (1964, 1967, 1968), has focused on problems related to community structure, diversity and stability in terms of natural selection acting upon genetic variability within the component populations of the system. Most studies based upon this approach assume that the community has reached some equilibrium state and that natural selection acts primarily toward optimizing ecologically important quantitative characters such as foraging ability, clutch size, etc. within this "ecological equilibrium" state. Many interesting developments in this field can be found in the MacArthur Memorial Symposium volume: Ecology and Evolution of Communities (ed. by Diamond and Cody, 1975). The power of this point of view can be seen in Maynard Smith's (1976, 1978) idea of an evolutionarily stable strategy. Lawlor and Maynard Smith (1976) provide one example of the power of using this approach in systems that are in obeying some ecological and genetic constraints on important fitness parameters. These are assumed to obey some fitness set constraint and be invulnerable to an evolutionarily stable strategy. Other attempts have been made which implicitly incorporate more realistic interactions into

Fisher's FTNS and Wright's model. Attempts to modify these theories to account for density dependence, age structure, competition and other nonlinear interactions are just beginning.

In order to to gain a clearer understanding of the effects of such ecological factors as density dependence and competition on the fitness of an organism, several authors (Roughgarden 1971, 1976, 1979; Anderson 1971; Leon 1974) have studied a coupled set of discrete-time difference equations of the form:

$$\Delta N_i = N_i (w_i - \bar{w}) = N_i (a_i - b_i N_T) \quad (4a)$$

$$\Delta p_i = p_i \frac{w_i - \bar{w}}{\bar{w}} = p_i \frac{[a_i - \bar{a}] - (b_i - \bar{b}) N_T}{1 + \bar{a} + \bar{b} N_T} \quad (4b)$$

Wright (1959). Where

N_i = density of i th gene

p_i = gene frequency i th gene

w_i = fitness function of the i 'th gene

$\bar{w}$ = average fitness function

Here a and b are ecological parameters related to density dependence, and N_T is the total population. Roughgarden (1971) (by computer-iteration) studied the time-dependent and stationary solutions of these equations in order to determine the initial conditions in which fixation or polymorphisms for "high r " or "low K " genes would occur. He also showed that evolution in a coarse-grained seasonal environment causes a stable polymorphism between high r and high K genes. Anderson (1971) showed that for ecological and genetic equilibrium:

$$dK(p)/dt = 0 \quad (5)$$

This implies that the equilibrium occurs at a relative maximum or minimum of the function $K(p)$ and gives the conditions under which K is increased. Thus Anderson was able to show that selection adjusts gene frequencies in such a way as to maximize certain important ecological parameters in his model. MacArthur (1962) used a system of differential equations to derive a similar result graphically. Demetrius (1975) developed an entropy-theoretic version of Fisher's FTNS. This allowed him to make predictions on how natural selection guides the evolution of ecological parameters in an age-structured population. Similarly, Charlesworth (1972) derives conditions which show that the malthusian parameter is maximized under selection in an age-structured population just as it is in the classical theory (by Fisher's FTNS). Building on the results of Roughgarden (1971) and Leon (1974), Leon and Charlesworth (1978) recently have derived several analogs to Fisher's FTNS for communities which exhibit density-dependence, competition, and mutualism. Roughgarden (1971, 1976, 1978) developed several results which predict community coevolution under purely density-dependent

selection.

Roughgarden (1979) made one of the first major efforts to explicitly integrate population genetics and ecology. Most of these authors derive their results from a system of the form (4) or on modifications of it (such as modification for multispecies interactions):

$$\Delta N_i = N_i (\bar{w}_i - 1) \quad (6a)$$

$$\Delta P_i = P_i \frac{(1 - P_i)}{2 \bar{w}_i} \frac{\partial \bar{w}_i}{\partial \tau} \quad (6b)$$

Here $\bar{w}_i$ is the average fitness for species i , and is now a function of N_T . It is important to recall several assumptions which underpin formulations using the system (6), or modifications thereof:

1. The values of the parameters are limited to the 'less sensitive' regions of parameter space. For example, Roughgarden (1971) must restrict r to the interval $(0,1)$ to avoid chaotic behavior, which often occurs in discrete systems of the form (6). May (1974a, 1975a) and Oster (1974, 1977) have shown some specific examples of chaos in particular ecological and genetic models. Asmussen and Feldman (1977) have shown that for various parameter values of the system (6) it is possible to obtain negative fitness values. In one case they note that negative fitness values can force the trajectories into negative gene frequencies, gene frequencies greater than one or negative population sizes. These sensitive regions of the parameter space may be important for understanding how rapid speciation events can manifest themselves in communities. Around critical parameter values, when the system is in a nonequilibrium state, transitions may occur in the community which may correspond to diverging populations or speciation events. Oster, Ipaktchi and Rocklin (1976) have demonstrated the sensitivity of certain parameter values in nonlinear difference equations when a phenotypic structure is included in the population dynamics. For a particular model involving the inheritance of a quantitative trait (Slatkin, 1978; Rocklin and Oster, 1975), they show that changing the per genic birth rates (hence influencing the r value) in situations of assortative mating can lead to bifurcations.
2. The models typically assume no frequency-dependent selection. In most cases, purely density-dependent selection is assumed, although Roughgarden (1976) and Levin and Udovic (1977) have extended the model to account for limited aspects of interspecific frequency-dependence. However, Roughgarden (1978) uses a system of the form (6) in his analysis of predator-prey coevolution which includes interspecific frequency dependence.

Many difficulties arise because the system cannot be analyzed in terms of its equilibrium behavior in the frequency-dependent case. Hence only a limited statement concerning the systems local stability can be made. Frequency-dependent selection will most likely cause multiple steady-states which cannot be adequately analyzed using local stability analysis. This is one kind of problem that we expect to study in detail. In Leon's (1974) competition model only interspecific interactions are assumed, so that comparison with many frequency dependent selection models in the population genetic and ecological literature (Clarke, 1972; Ayala and Campbell, 1974) is precluded. Similarly, Leon and Charlesworth's (1978) derivation of ecological versions of FFTNS applied only to systems such as (5) and (6) in which $\bar{W}_i(N_i)$ is a function only of the equilibrium densities. Thus they must assume that selection is sufficiently weak so that population densities come into approximate ecological equilibrium, and then change slowly in response to gene frequency changes. They recognize that the method breaks down if the population is ecologically unstable for certain gene frequencies.

3. Difference equation models are based on the assumption of discrete, nonoverlapping generations, such as occur in annual plants and some insect species. For organisms reproducing continuously, these models are undoubtedly unrealistic. Templeton's (op. cit.) founder theory of speciation predicts that populations reproducing in discrete generations have a lower probability of undergoing a genetic transilience. One important feature is that the differences between per genic fertilities and death rates are not explicitly included in the model. While this simplifies the derivation of ecological parameters by allowing one to invoke the assumption of random mating, This feature of the model precludes interpretation of the parameters in terms of the mating structure, fecundities, and fertilities of the population. Recently a number of authors have sought to develop differential equation (and P.D.E) models for genetic analysis (Nagylaki and Crow, 1974; Nagylaki, 1977; Cornette, 1975), although few have attempted to incorporate ecological interactions such as density-dependence and competition.

3.2 Alternative Models

3.2.1 Models Describing Evolutionary Dynamics -

We can distinguish several mechanisms by which populations may evolve in time. Among the most important are the following:

1. Genetic processes: all populations are composed of individuals which vary genetically from one another. Even in asexual populations, genetic variation appears via mutation.

2. Competitive processes, both intraspecific and interspecific: These processes occur because of the varying abundance of the resources in a particular habitat. Some resources are more limited than others, hence organisms evolve particular strategies as the available resources change. The resources can be viewed in terms of the nature of the interaction involved (exploitative or interference) or in terms of energy required to utilize the resources (Schoener, 1973; 1974a).
3. Regulatory processes: The effects of regulatory processes are somewhat controversial. The arguments generally focus on the influence on the total population size of such factors as the behavioral and physiological activities of individuals, and on how these factors evolve. Many arguments invoke kin selection or group selection (Wilson, 1975). The possibility of group selection as a mechanism of community evolution has been investigated only recently from the theoretical point of view (Levins, 1970; Wilson, 1975), although computer simulations have shown that nonlinear interactions can favor part of the population which affect the survival of the entire population (Gilpin, 1975). On firmer theoretical ground is the theory of kin selection, which has recently been extended to predict the evolution of caste strategies and polymorphisms in ants (Oster and Wilson, 1978).
4. Communication processes: Populations communicate between local areas after dispersal by migration using sensing devices such as air movements and odors (Richardson and Johnston, 1975; Johnston, Appendix B). This communication affects the dynamics since populations under such dispersal exhibit spatial interactions as well as competitive or other multispecies interactions. Pheromonal effects also modify the mating structure of the population (Averhoff and Richardson 1974, 1977, 1980). These effects on the evolution of populations have only recently come under investigation (Richardson, 1974) and we expect to model this phenomenon as a mechanism of population diversification and speciation.

To confront some of the difficulties encountered in the difference-equation models of the preceding section, we adopt a more general model which will ultimately incorporate all the mechanistic elements outlined above. Under appropriate assumptions, this model will reduce to corresponding discrete-generation analogs (see Table 1). In this way the more general model can be benchmarked by comparing its predictions to those of simpler models already studied in the literature (e.g. Roughgarden 1971, 1976; Anderson 1971; Leon 1974). By formulating our models as differential equations we can utilize powerful analytical and numerical methods available for solving systems of nonlinear differential equations (see section 3.3.1). The formulation we follow is based upon that used by Nagylaki and Crow (1974) and Nagylaki (1977) in which they derive a number of continuous selection models for different genetic states: nonrandom mating, multiple alleles at a single locus, gametic selection, no dominance, mutation and migration. Using this same approach we derive a number of models incorporating competition among

species for resources. Related work using this approach treats density- and frequency-dependence (Smouse, 1976) and competition (Rocklin and Oster, 1975). Cornette (1975) has shown that the work of Nagylaki and Crow (1974) and Charlesworth (1970) can be combined to produce a general partial differential equation containing terms for per capita fertilities and death rates at different ages, thus incorporating age structure. These models are shown in Table 2 in addition to some of the models which we consider. Although these models appear complicated, there are a number of advantages that are obtained by working with nonlinear differential equations. With these models we can also investigate other genetic effects such as mutation, population subdivision, intraspecific frequency dependence and phyletic species packing. These are topics which until quite recently have not been investigated (Allen, 1976b; Smouse, 1976) and still have a sketchy theoretical basis.

In the following discussion we outline the construction of general ecological and genetic models which incorporate both population density and genetic aspects. Also we compare our research plans to previous approaches in this field.

In general, we consider systems of the form:

$$\dot{N} = F(N, p) \quad (7a)$$

$$\dot{p} = G(N, p) \quad (7b)$$

These equations for total population N and gene frequency p can be obtained by summing over the separate differential equations for the corresponding genotypic variables N_{ij} and p_{ij} . The functions F and G can represent any ecological or genetic interaction (see Tables 2 and 3), and are generally nonlinear in N and p . The functions chosen reflect the theoretical or experimental interest of the investigator. In addition to being nonlinear, the differential equations (7) will contain many parameters and "internal" variables that will determine the dynamics of the system (Oster et. al., 1976; Schoener, 1973; Levins, 1968).

A principal aim of our study is to determine how evolution affects the dynamics of a system by causing changes in important ecological parameters. We want to investigate the mechanisms by which a phenotype in a population 'adapts' to a particular evolutionary pressure. The nature of such an adaptation is difficult to investigate, for one must consider whether evolution ever leads to an optimally adapted phenotype. What is evolution optimizing? Does it 'optimize' a phenotype differently in a community in which competition for resources is high (as in a tightly packed community) than for a community in which a competitive vacuum exists? We intend to study several ecological situations in which it is not obvious at all what, if anything, is being optimized. The clear implication here is that, in order to understand how coevolution and speciation occurs one must explicitly write the equations of motion for the community dynamics and determine the conditions under which coevolution, speciation and ecological divergence can occur. Traditionally population geneticists have gotten out of this dilemma by vaguely defining 'fitness' as the trait which is optimized. As we shall see from this study, an organism's 'fitness' comprises several, very complicated components, some of which are antagonistic to others. One

aspect which must be examined carefully concerns the meaning of adaptation in the context of an organism's niche in the community as that community is itself changing, through environmental fluctuations, internal fluctuations and extinction of species. Species might be thought of as trying to track the environment through niche space and always somewhat lagging behind it (Lewontin, 1978). This is somewhat in contrast to the classical theories of population genetics (as presented in section 3.1.2.1), although Fisher (1958) gives a very readable account on the nature of adaptation. Wright (1969), however, seems to assume that a stable adaptive peak is reached at which fitness is maximized by evolution. Indeed, Kimura (1958) defines what might be called a 'potential function' for the maximization of an organism's fitness. This is likely to be only in systems in which the governing equations are simple. When the equations include nonlinear interactions, a variety of qualitatively new features are possible. For example, a typical result of nonlinearity is the appearance of multiple steady states which exhibit different types of behavior. Depending upon internal fluctuations and as parameters undergo changes, a system described by such an equation can evolve in a variety of ways. Let us now turn to the specific types of models and methods which will play a major role in our studies of the situations outlined in Table 2. We present several cases in which models are to be analyzed and the possible kinds of evolution examined. This will be done in three areas: density- and frequency-dependent evolution; evolution in competitive systems; coevolution and phyletic species packing.

3.2.1.1 Density And Frequency Dependent Evolution -

Density- and frequency-dependent selection (denoted in the following by DDS and FDS, respectively) have been investigated extensively in recent years (Roughgarden, 1971; Cockerham et. al., 1972; Smouse, 1976; Slatkin, 1978). Most of these authors treat separately the effects of density and frequency dependence. Smouse (1976) however, derived a system of differential equations, based upon a Lotka-Volterra model, which contained both DDS and FDS. In the most complex case, the diploid sexual case for DDS and FDS, the model defied rigorous global analysis, although a number of interesting steady-state situations of interest were investigated. One interesting feature that has yet to be investigated is the possibility of multiple steady states. With appropriate assumptions made about the mating structure of the population, steady-state equations of cubic or higher order can result. Multiple steady- states may be relevant in several situations to us, for example in understanding the nature of polymorphisms and boundary equilibria. In trying to understand how 'r' and 'K' selected alleles evolve in a community we might consider the possibilities of rapid 'jumps' or 'discontinuities' of the component genotypic populations as the genotype parameters evolve across parameter space under selective pressures. In such a situation a number of possibilities exist for coexistence of different polymorphic states of alleles.

The current importance of the concepts of 'r' and 'K' selection lies in the fact that they involve genetic as well as ecological changes in response to selective pressures. This notion has not been widely

appreciated, although a few models involving density-dependent selective values have been investigated (Roughgarden, 1971; Anderson, 1971; Leon, 1974). Nevertheless, the conditions whereby 'r'- and 'K'-selected alleles are fixed remain unknown, as indicated above. Furthermore, it is not known what fitness parameter, if any, might be optimized in frequency- and density-dependent evolution.

A simple example of such a model can be derived by writing the logistic equation as a birth and death process:

$$\frac{dN}{dt} = N[(\bar{b} - \bar{k}_b N) - (\bar{d} - \bar{k}_d N)] \quad (8)$$

To study the effects of genetic structure on the population's growth, we must treat explicitly the dependence of individual genotypes on the birth and death parameters. In the simplest case we introduce the most basic laws of Mendelian genetics into a density dependent model. To do this we assume:

1. the interactions within the species are governed by a phenotypic character controlled by a single locus with two alleles,
2. the population is large enough that all individual genotypes can find a mate,
3. simple Mendelian dominance governs the trait.

One model which incorporates these features is the following set of equations for genotypic population N_{ij} :

$$\frac{1}{N} \frac{dN_{ij}}{dt} = \sum_{k\ell} p_{ik} p_{j\ell} (b_{ijk\ell} - k_{ijk\ell} N) - p_{ij} (d_{ij} + k_{ij} N) \quad (9)$$

where the genotype frequencies are defined $p_{ij} = N_{ij}/N$.

This system is a continuous analog of the discrete model of Roughgarden (1971) and Anderson (1971). The connection can be made explicit if random mating is assumed and frequency-dependence omitted. With a single locus and two alleles, for example, equation (9) can be written in the form

$$\begin{aligned} \frac{dN_{11}}{dt} &= p_{11} r_{11} N (1 - N/k_{11}) \\ \frac{dN_{12}}{dt} &= p_{12} r_{12} N (1 - N/k_{12}) \\ \frac{dN_{22}}{dt} &= p_{22} r_{22} N (1 - N/k_{22}) \end{aligned} \quad (10)$$

One can therefore think of an equation describing density dependent growth as being an average over the genetic structure of a population in which individual genotypes can have different selective values. Such a model would be expected to behave differently under different selective regimes. The most familiar example appears in evolutionary ecology as the concept of 'r' and 'K' selection (MacArthur 1962; MacArthur and Wilson 1967). Pianka (1970) showed some probable correlates which an r or K selected organism should exhibit. Much analysis has been done to determine the reproductive strategy of organisms lying on the r-K continuum (Pianka, 1972; Stearns, 1975). However, our approach is more in the spirit of Roughgarden (1971, 1976), in that we wish to understand the dynamics which underlie the r-K selection theory in terms of genetic variables in addition to ecological parameters. In this way we can begin to make connections between ecological and evolutionary processes.

In this section we have concentrated on density-dependent selection models, but other types of interactions such as competition and predation can be studied using these same techniques (Rocklin and Oster, 1975; Smouse, 1976). We can easily reformulate the models which include resource dynamics (see section 3.2.1.2 and the tables) to incorporate diploid genetics. Several models that do this are listed in Table 2 and variations on some of these appear in Table 3. Many of the models in Table 3 can be interpreted as being differential equation analogs to difference equation models incorporating ecological and genetic interactions in the literature (for a sampling of these see Table 1). Comparing the advantages of working with each one, we can develop criteria, such those listed in Tables 4 and 5, to evaluate the models according to their potential value in explaining such ideas as phyletic species packing, the dynamics of evolving community stability, and the effects of mutation and population subdivision in a coarse-grained environment. Each system has its advantages, although the use of differential equations to describe genetic and speciation processes has only recently started (Nagylaki and Crow, 1974; Nagylaki, 1977; Cornette, 1975). Using the techniques developed to derive the models in this and the following sections (see also Table 2) we expect to build models of habitat selection and phyletic species packing.

3.2.1.2 Evolution In Competitive Systems -

In this section we consider models which will take into account resource dynamics, mutations and population subdivision. With alternative versions of the logistic equation modified to include multispecies interactions, these systems can then be parameterized genetically and investigated to determine the resulting evolutionary features. Since these alternative models include parameters reflecting the ability of genotypes to utilize a specific resource or substrate, we can study the evolution of specialist or generalist species in the face of a number of ecological interactions. Under certain assumptions it will be possible to relate our results to MacArthur's (1970) idea of the number of species which can be packed into a community.

We want to describe the population and evolutionary dynamics of organisms undergoing the above processes. To derive a simple equation

which can take these processes into account, we assume the existence of a food or substrate, A that is used by members of the population, x, and who are produced at a rate kAx and die at a rate dx .

If the resource A were unlimited, then exponential growth would take place if $kA > d$ or exponential death when $kA < d$. With limited resources, we make the simplest assumption that A is recycled through the community as x dies therefore it follows that there is a conservation condition for the total amount of organic matter in the community

$$A + x = N \quad (11)$$

With this condition the dynamics of the population is given by the equation

$$\dot{x} = kAx - dx = kx(N - x) - dx \quad (12)$$

Clearly this equation is a variation of the logistic equation appropriate to finite resources. The steady-state population is given by

$$\hat{x} = N - d/k$$

Here, the Malthusian parameter or 'biotic potential,' $r = b - d$, is represented as $kN - d$. If we reparameterize eq. (11) in a form analogous to equation (8), then we can introduce genetics into the model (cf., eq. (9)) to get eq. (2) of Table 2. This procedure is followed systematically for all the models of Table 2. These results are analogous to those in Table 3. Similar derivations can be made to define a system of equations of the form in Table 3 which are analogues to the difference equations which appear in Table 1. Research is now in progress to determine if simulations produce results analogous to those of Roughgarden (1971) and Anderson (1971). Some results with this system (eq. (11)) have been obtained (Allen, 1976a) in which the system is extended to two competitors as shown in Table 3.

3.2.1.3 Phyletic Species Packing And Co-Evolution -

The idea of species packing was introduced by MacArthur (1969, 1970) to describe the effects of competition of species and to attempt to define some quantity Q, that could be minimized by competitors. He used the idea of species packing to show that if Q is minimized by competition then one can predict the overlap of competitors and how closely in resource utilization they could be in a particular type of environment. Further, MacArthur (1970) noted the evolutionary implications of species packing: "When it exists, the form Q plays a role analogous to fitness in classical natural selection theory." He noted however, that this view, at least in the formulation he originally derived it only applies to a static equilibrium. Recent field work appears to indicate however, a more general evolutionary implication of the species packing idea. For example, Richardson (1974) developed a hypothesis that indicates sympatric speciation (in addition to colonization) can act as a mechanism of 'species packing' during the

evolution of a community. Although colonization clearly plays the key role of increasing the number of species on impoverished islands, the later stages of species packing may be through speciation. If this is true, community structure, optimal utilization of resources, and other ecological aspects of a biome may be recognized as products of the evolutionary process of speciation and genetic adaptation. Richardson and Smouse (1975) termed this type of community co-evolution 'phyletic species packing.'

The models of community structure in tables 2 and 3 are designed to describe the evolution of resource utilization patterns of competing species and hence determine patterns of phyletic species packing. With these models it is possible to assess the impact of speciation on the evolution of various ecological and genetic parameters (see the procedures, Section 3.3).

By studying a phenotype's resource utilization distribution we can make connections with the food niche, habitat niche, etc., i.e. whatever niche dimensions are most important in affecting the phenotype's fitness. There have been a large number of field studies showing how character divergence is caused by ecological factors (Karr and James, 1975; Huey and Pianka, 1974; Pianka, 1976). Most of these studies were done by correlating some morphological character, such as jaw size with a particular span of the resource distribution (Roughgarden, 1972; Schoener, 1974b). Data is then gathered along the most important niche dimensions and 'overlaps' are calculated between competing species to determine the part of the resource spectrum in which competition is most intense. Along any given resource spectrum it is assumed that pressures (ecological and evolutionary) leading to the avoidance of interspecific competition dictate certain patterns (for example, the hypothesis that the ratio of demand of a resource to its supply is constant). Determining the degree of 'packing' of competing species is important and related studies involving resource-partitioning among competing species or niche segregation have attracted a great deal of interest years (MacArthur, 1972; Cody, 1974; Schoener, 1974b; Pianka, 1976). Such studies are important because the precise mechanisms by which available resources are divided among members of a community must be known before determinants of species diversity and community structure can be fully understood.

There is a large body of theoretical work which predicts the ecological aspects of niche breadth and species packing (MacArthur, 1969, 1970; May and MacArthur, 1972; Pianka, 1974) but very few studies incorporating evolutionary and genetic processes. It is easy to make intuitive and verbally constructed models predicting that in a community of competing species, natural selection will tend to relax competition by separating the utilization functions. Thus, one can say that where a species lives together with a competitor, individuals of a phenotype which utilizes the part of the resource spectrum not used by the competitor will have a higher fitness than an individual of a phenotype which uses the same part of the resources as the competing species. What is more difficult, however, is to mathematically formulate models which explicitly show how selection will act on populations (which are now assumed to have some genetic structure) involved in competition for resources. Roughgarden (1972) has given us a start in this direction but

much more research is needed to explore the dynamics of such evolutionary pressures such as phyletic species packing. In a very significant paper Roughgarden (1976) has explored a number of genetic and coevolutionary processes among competing species to study resource partitioning. He derives a set of principles that describe the evolution of parameters in ecological models. His results are interesting and provide an excellent benchmark for our study of phyletic species packing. Although his formulation is quite general, it assumes the coevolutionary process leads to some kind of evolutionary equilibrium at which time the competing species maximize their equilibrium population size. In our studies we shall explore many situations in which the communities are perturbed far from equilibrium and we shall determine and describe the mechanism by which ecological divergence and rapid speciation events occur. In our study of the evolution of community interactions we will explore the mechanisms that maintain community stability and species diversity.

Basic Model

To describe community evolution and dynamics of phyletic species packing we begin with a general model

$$\frac{dx_i}{dt} = k_i x_i \left[N_i - \sum_j \beta_{ij} x_j \right] - d x_i + F_c(\{x_j\}) + F_r(\{x_j\}) + F_n(\{x_j\}, \{x_j^e\}) \quad (13)$$

Where,

F_c , F_r = nonlinear functions which describe the rate of competition implied by eq. (14) and the rate of regulation.

F_n = Function describing migration or movement dependent upon x_j

β_{ij} = parameter describing effectiveness of species i using resource

This system can be extended to represent genetic interactions as shown (above) by the special case of single species growth, although the equations become considerably more complex. In the case of multispecies interactions, numerical simulations can be run to determine the evolution of interactions in a community in a number of situations. Allen (1976b) has done some interesting work using the system (eq. 13) by introducing diploid genetics, and, in the asexual case, by using mutations to provide genetic variation. He also has been able to develop a possible criterion to predict the successful invasion of communities composed of competitors by a mutant which is based solely on the structural stability of the new system of equations. This "evolutionary criterion" was linked to Maynard Smith's idea of an evolutionary stable strategy (ESS) by Schaffer (1977). Although Roughgarden (1979) takes the first step and relates the results of a lemma on interspecific frequency dependent selection on the boundary equilibria of a system (of the form in Table 1) to the idea of an ESS, the relationships between an ESS and evolutionary dynamical systems are not fully known.

We have been able to use the system to indicate a number of models potentially useful for predicting community evolution. The structure of the general system [eq. (13)] lends itself to a number of modifications to study some of the dynamical processes previously listed: genetic,

competition, regulatory, and communication. Although (13) is general enough to cover a wide variety of behavior, we now consider its use in understanding the theoretical implications of species packing on community dynamics and stability. In this context we will outline our general approach to the mathematical modeling of systems which may possess high degrees of nonlinearity and complexity, and we will introduce the analytical and numerical methods employed in our investigations.

We treat a number of clusters of related subspecies, each of which may contain units (i.e., classes of subspecies or gamodemes) which are reproductively isolated. Different clusters are expected to be strongly interacting (i.e., competitive) in relatively small regions of niche overlap, while members of a cluster (related gamodemes) will be weakly interacting in many regions of niche overlap. Different clusters might represent different taxonomic families, for example, and may have intense competitive interactions in very limited parts of their niche hypervolumes, including predator-prey relationships. Members of a cluster would likely not compete in this way, having evolved by such processes as host shift, temporal shift, and the like. As an initial effort to describe such a system quantitatively, we consider the following models, and begin with the simplest situation:

Case I. Reproductively isolated species (no interspecific transitions). The population X of species i is given by the following equation:

$$\frac{dx_i}{dt} = k_i x_i \sum_{\alpha} \beta_{\alpha i} (N_{\alpha} - \sum_j \beta_{\alpha j} x_j) - d_i x_i \quad (14)$$

Here K_i and d_i are intrinsic birth and death rates, respectively, of species i . The species index i is generic, and may actually be a two parameter index representing individual genotypes, for example. Species i utilizes a spectrum of resources $A = \{\alpha\}$, each resource having carrying capacity N_{α} . The effectiveness of species i in utilizing resource α is $\beta_{\alpha i}$. From this model it is straight forward to derive steady-state communities and determine their stability with respect to the introduction of new species in terms of basic ecological and genetic parameters.

Case II. Modification through mutation. Mutations $i \rightarrow j$ are of two types according to whether they

1. change the utilization efficiency within the same resource spectrum

$$\beta_{\alpha j} = \beta_{\alpha i} + \Delta \beta_{\alpha i}$$

or

2. change the resource spectrum

$$A_j = \{\alpha\}_j \neq A_i$$

Clearly the effect of mutations is to add new species to the spectrum, and hence new equations to the model. We can picture how a mutant can coexist or displace a species as:

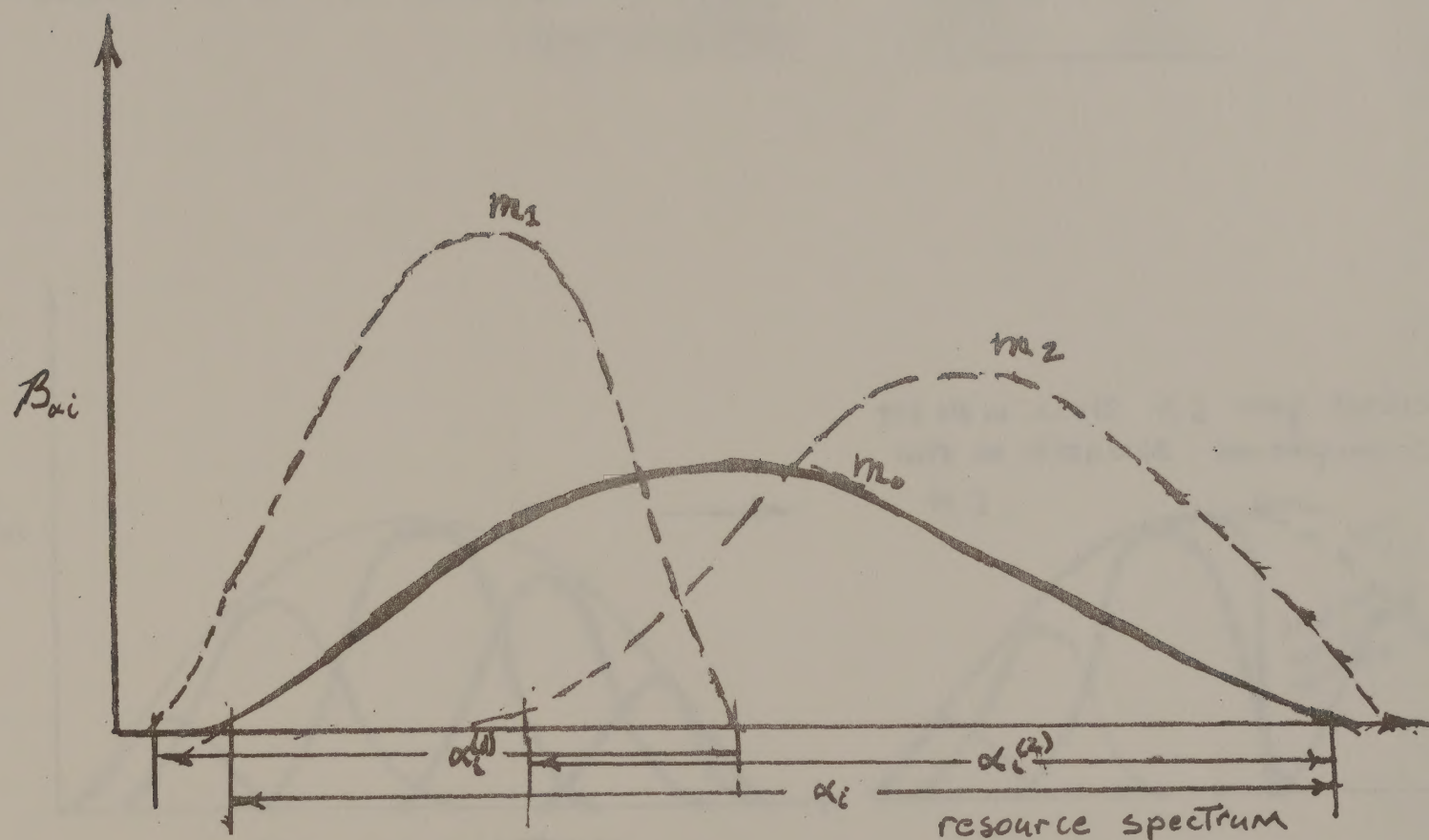


Figure 1

Furthermore, with these equations we can define a resource utilization or niche axis, s , and a width of the resource spectrum exploited by each species.

Case III. Subclasses within reproductive units. If u denotes a reproductive unit, then eq. (14) becomes

$$\frac{dx_{i,u}}{dt} = \sum_k k_k^{(u)} x_{u,k} \sum \beta_{\alpha,k}^{(u)} (N_{\alpha} - \sum \beta_{\alpha,j} x_{v,j}) - d_i x_{v,i}^{(u)} \quad (15)$$

Here the sum over k accounts for the possibility of producing subspecies i as an offspring of subspecies k . The superscript (u) indicates the quantities which will in general vary with u as well. We can write this equation more simply in the schematic form

$$\frac{dx_{i,u}}{dt} = \sum_k k_k^{(u)} x_{u,k} E_k^{(u)} - d_i x_{u,i}^{(u)} \quad (16)$$

where $E_k^{(u)}$ is the totality of resources available to subspecies k of reproductive unit u .

Case IV. Speciation. To the possibilities of Case II we add a third: mutations can lead to reproductive isolation, and hence to new model equations representing a new reproductive unit (i.e. speciation). Consider the case of introducing reproductive unit u which should depend on the mutating class i being already fairly specialized and overlapping little with the rest of the gamodemes.

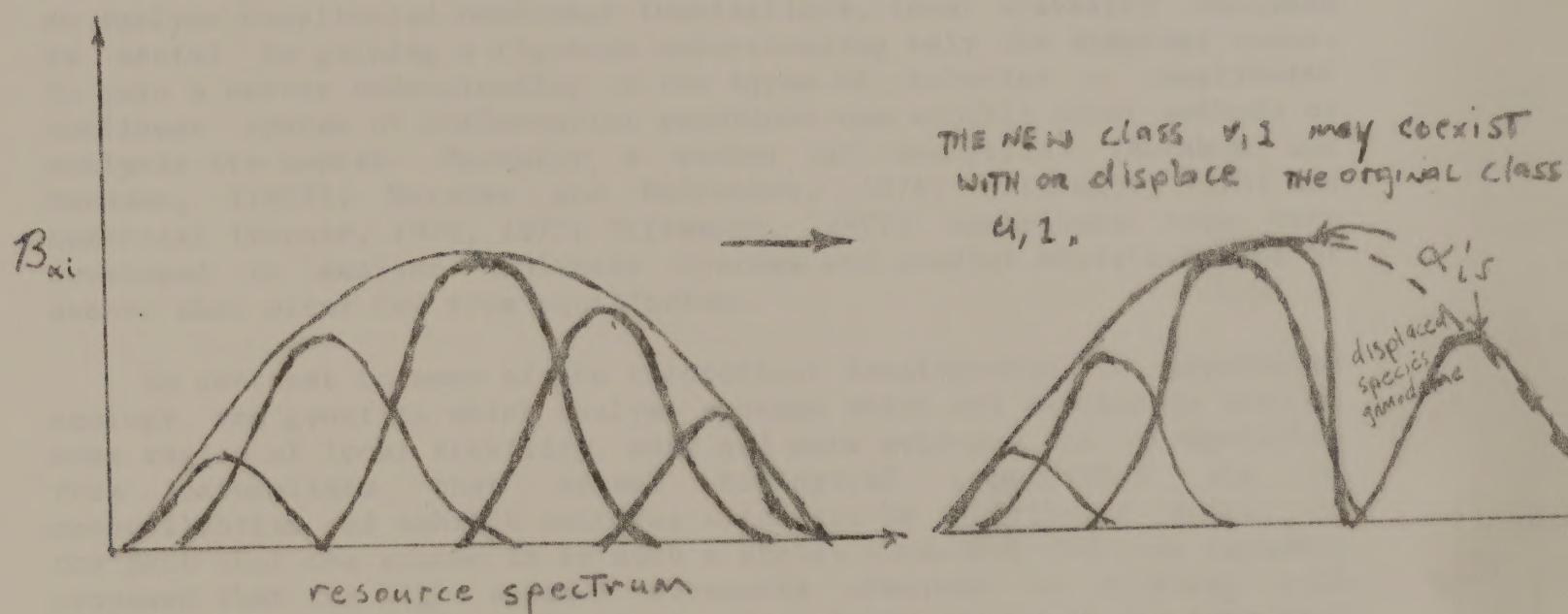


Figure 2

If u now mutates to further exploit the marginal resource, via $m(1)$ and/or $m(2)$, as for example in Case II, then it is likely to survive. However, to find the actual mechanism that causes the outcome we can analyze the models. Although the mathematics rapidly becomes cumbersome and analytical results will be done only in the simplest places, in the complex situations tests of the various cases with respect to internal fluctuations can be carried out since the mutations and evolution can be handled using stochastic simulation methods, while the larger populations can be treated deterministically (see Section 3.3). Extensions of the models to handle separate clusters is straight forward since inter-cluster interactions are much simpler. Extensions to treat genetic recombination effects, non-allelic interactions and multiple-loci are possible.

3.3 Procedures And Work Plan

3.3.1 Theoretical Interpretation And Methodology -

The concept of the stability of an ecological community is one of the most interesting and challenging problems that exists in ecology. Most of the work done in the past has been based on the assumption that communities are in equilibrium and if random perturbations occur, they will return to the same region of local stability. Thus the use of local stability analysis has been implicit in the writings of many ecologists such as MacArthur (1969, 1970), May (1974), May and MacArthur (1972), and Roughgarden (1979) in studies investigating species packing or limiting similarity. These studies are important starting points for any analysis of species packing, but in trying to understand evolutionary effects which occur when a community is far from equilibrium, the results are inapplicable. While useful as a beginning mathematical tool to analyze complicated nonlinear interactions, local stability analysis is useful in gaining a rigorous understanding only the simplest cases. To gain a better understanding of the types of behavior a complicated nonlinear system of differential equations can exhibit other methods of analysis are needed. Recently a number of analytical (Abraham and Marsden, (1978); Marsden and McCracken, 1976; Sattinger, 1973) and numerical (Turner, 1975, 1977; Gillespie, 1977) techniques have been developed to analyze nonlinear systems and predict their behavior at states that occur far from equilibrium.

In contrast to many of the theoretical developments in population ecology and genetics which analyze systems which are assumed to stay in some region of local stability, more and more evidence is accumulating from naturalists that actual biological communities are in nonequilibrium and exhibit patterns which can be attributed solely to the fact that the system is in such a state. Connell (1978) has recently proposed that the high species diversity observed in tropical rain forests and coral reef communities is maintained due to the fact that the community is perturbed far from equilibrium. Hubbell (1979) in studying the spatial dynamics in a tropical rain forest observed that since tropical trees are clumped, and not evenly spaced, we must alter our current conception of the organizational dynamics of such communities. In evaluating whether or not forest communities are at equilibrium Hubbell observes that our understanding of community organization would profit from more study of processes of disturbance, immigration, and local extinction, in conjunction with the more traditional studies of biotic interactions of species (such as competition, niche differentiation and seed predation). The models described above can be analyzed to determine the effects of fluctuations in the nonequilibrium states and the resulting formation of patterns (if any) that would be predicted to occur in such communities described by Connell and Hubbell. Before we describe how this is done, however look at the evolutionary and biological implications of another type of stability: structural stability.

Richardson and Smouse (1975) examined field data for evidence of the effects of phyletic species packing and interpreted the present communities of Hawaiian *Drosophila* competitors as having evolved by the ability of different species and gamodemes to invade the community

depending on the community's level of saturation or packing. Further, they evaluated the resulting stability of the community from such an invasion, considering stability of two types, numeric stability and 'saturation' stability. Numeric stability was defined and related to what might normally be called local or Lyapunov stability, while saturation denoted the tendency to resist invasive colonization, which is related to MacArthur's (1972) use of coexistence and invasibility. Since these analyses were dealing with the Lotka-Volterra competition equations, only approximations and intuitive guesses could be made as to how the communities evolved in terms of phyletic species packing. Using the methods do derive equations described in Tables 2 and 3 and the general basic model described above, we can go somewhat beyond the linearized analysis and suggest a broader definition to community stability. It is more closely to what might be call the 'resilience' of a community to respond to large structural perturbations (Holling, 1973), although in our case it is more specifically applied to the evolution of related competitors. As we shall explain below, this idea is related to the idea of the structural stability of a dynamical system. We now follow with a broad look at two different aspects of procedures for analyzing these complicated systems: deterministic methods and stochastic methods. Stability properties can be related to the ecological and genetic parameters k_i , β_{ai} , and d_i for each species, and to the resources available, N_a . With resource competition explicitly in the equations we expect to determine and extend some of the basic results of of species packing models to situations that involve genetic transilience, speciation, and phyletic species packing.

3.3.1.1 Deterministic Methods -

Once a specific macroscopic model is adopted, the first step is to determine its steady-states and to assess the stability properties of these states with respect to changes in the genetic, phenotypic, and environmental parameters which define the model system. One possibility is always that there is a unique steady state with a weak dependence on parameter values resulting in a slow, continuous change in the system as parameters evolve. Of greater interest then this simplest case are systems which can experience discontinuous shifts in behavior for small changes in parameter values. Among the possibilities for qualitative change as determined by linear stability analysis, are the following:

(1) The most obvious consequence of nonlinearity is the possibility of multiple solutions of the governing differential equations. Here we take the view that the underlying ideas are best illustrated through actual examples of immediate interest. Therefore we consider the problem of determining the cause of insect pest outbreaks such as occur in screwworm populations. In this case we ignore competition and higher-order interactions to make the explanation clearer; these will be introduced later in our explicit work under this proposal. Consider the case of a possible genetic transilience in a cryptic screwworm gamodeme such as has been observed in experimental field work. Once suitable model equations are adopted which can occur for the qualitative features of the system (e.g. Equation IId in Table 2) we construct a bifurcation diagram by linearizing about the steady state(s) of the system. An

example might be Figure 3 in the space of a parameter b .

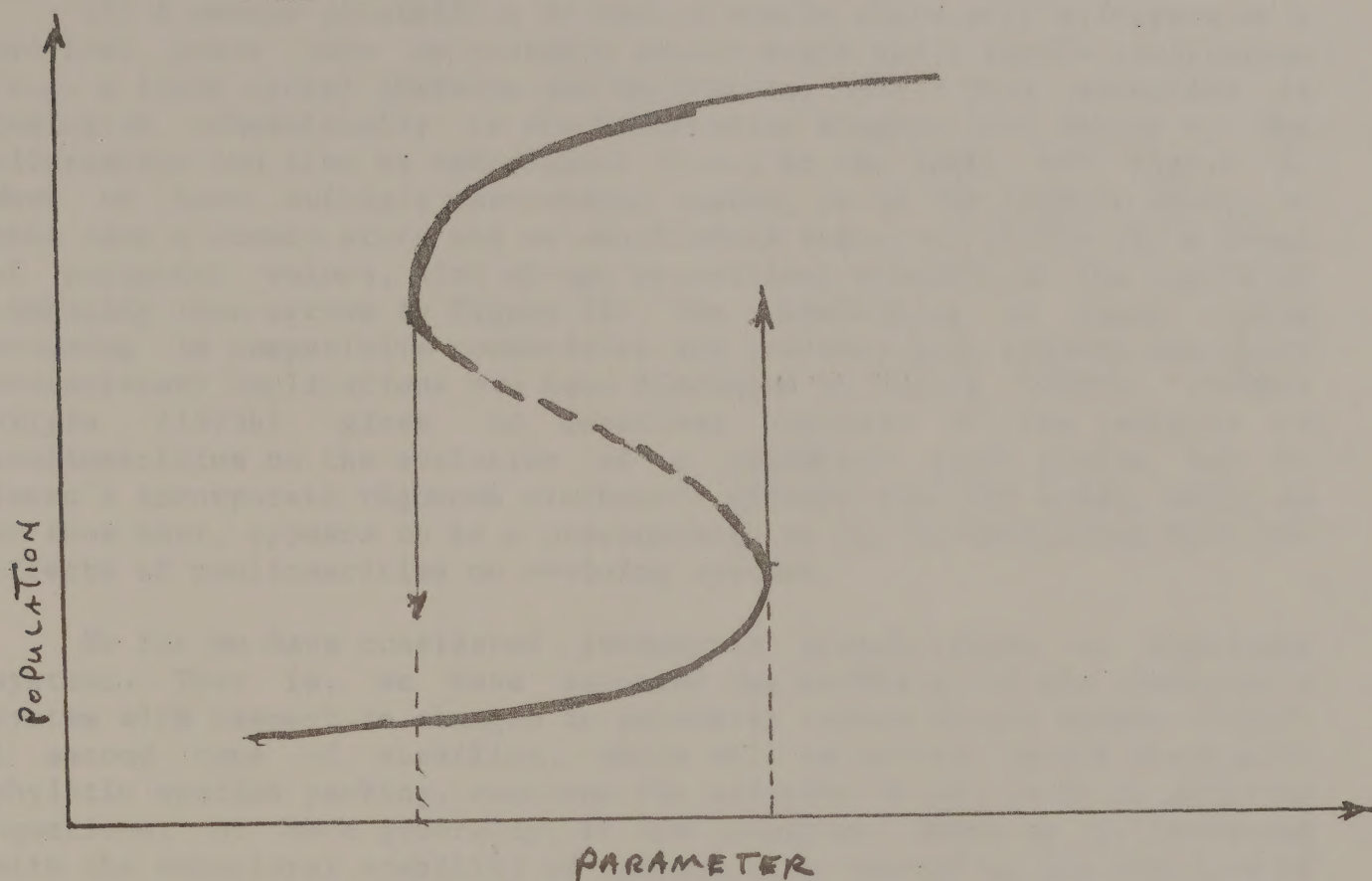


Figure 3

In this figure the region inside the curve is a region of multiple steady states. Typically in such models the upper and lower branches are stable and the middle are unstable. Therefore, as the parameter changes, discontinuous transitions between the stable branches would occur at their limits of macroscopic stability (arrows Figure 3). In the presence of internal fluctuations or external noise, the jump may occur before the stability limit is reached. Hence the importance of random or stochastic events as the evolution of systems, a point which will be addressed further below.

We are interested in studying the dynamics of this system, especially the effects of the nonlinearities upon the system in this hypothetical case. We want to determine those cases that could cause the cryptic species to ecologically diverge or give rise to a new species or some type of radical restructuring of the gene pool. As the environment changes (e.g. the parameter b), the species niche, which can be related to its adaptive 'topology' also, changes so as to track its environment. Now, as the population evolves along the parameter space, at some point, (e.g., critical value b), a new event can occur that drives the system to a new state. This new 'state' of the community could correspond to a pest outbreak, or some other explosive phenomenon. We intend to study the dynamics of such behavior in ecological communities and be able to give the qualitative conditions under which such events could occur. Our work in studying *Drosophila*, ticks and screwworms could serve as a starting point once we identify the most basic measurable genetic and

ecological parameters which are relevant to the theoretical model.

(2) A second possibility is that a stable state will bifurcate at a critical point into an unstable steady state and a stable oscillation (e.g. a limit cycle) (Marsden and MacCracken, 1976). This situation is indicated schematically in the bifurcation diagram (see Figure 4). The bifurcation can also be subcritical (i.e., to the left): see Figure 5. Here we have multiple macroscopic states, as in the example above, in this case a steady state and an oscillatory state are stable for a range of parameter values, with abrupt transitions possible at the limits of stability (see arrows in Figure 5). The possibility of limit cycles occurring in competitive communities and predator-prey systems and their evolutionary implications has been discussed by Gilpin (1975a, 1975b). Gilpin (1975b) gives an excellent analysis of the effects of nonlinearities on the evolution of a predator-prey system but he doesn't incorporate rigorous stochastic effects into his model, which as we show next, appears to be a prerequisite to any investigation into the effects of nonlinearities on evolving systems.

So far we have considered parametric instabilities in nonlinear systems. That is, we have assessed the stability of the states of a system with respect to changes in parameter values of the system itself. A second type of stability, which will be crucial to our studies of phyletic species packing, concerns the addition of new terms to existing equations, or more generally, to new equations. Hence we are concerned with the structural stability of systems with respect to the addition of new species via speciation or colonization. An ecological example of this type has been treated by Allen (1976). For a competitive system with one allele, he examined the stability of the system's steady state with respect to mutation, and derived conditions under which the mutant dies out, coexists with the original species, or displaces it within its niche. Similar arguments and methods will be important in our studies of the systems outlined above.

3.3.1.2 Stochastic Methods -

The effects of inevitable random influences on population dynamics are beyond the reach of deterministic differential (or difference) equations. Drawing the experience of one of us (J.S.T.) in modeling the dynamics and evolution of chemical systems, we will employ several methods developed for chemical kinetics which are especially suited to problems of population dynamics and evolution. Let us now formulate the problem of randomness in more detail, and introduce the principle methods in the process.

The Need for a Stochastic Description

A statistical (or stochastic) theoretical approach to rate processes such as chemical kinetics and population dynamics is motivated by the need to take into account various random elements of the systems of interest which render deterministic methods inadequate. Such random elements can take a variety of forms, and may arise at any level of

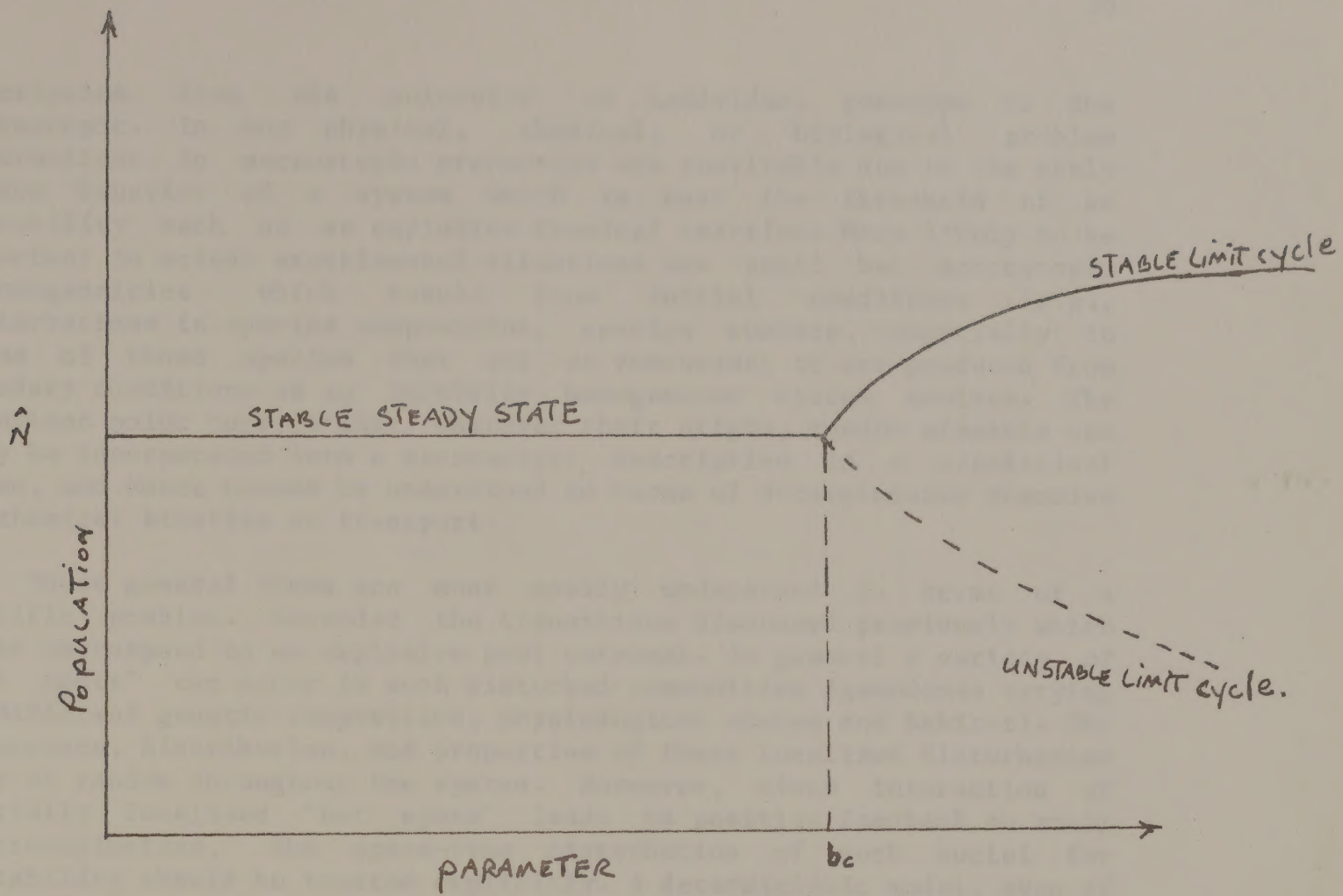


Figure 4

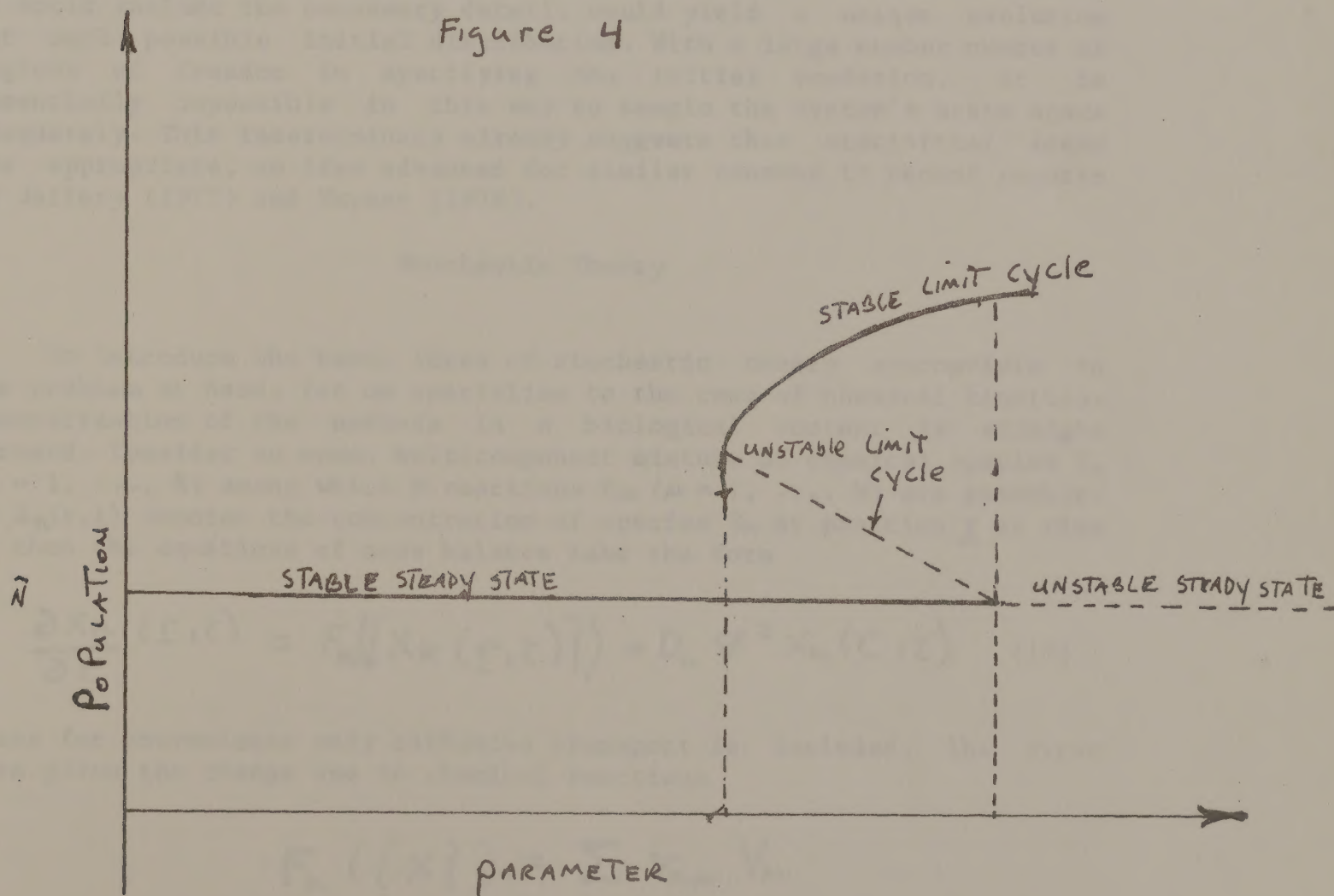


Figure 5

description from the molecular or individual genotype to the macroscopic. In any physical, chemical, or biological problem fluctuations in macroscopic properties are inevitable due to the truly random behavior of a system which is near the threshold of an instability such as an explosive chemical reaction. More likely to be important in actual experimental situations are small but macroscopic inhomogeneities which result from initial conditions (e.g., perturbations in species composition, species numbers, especially in terms of those species that act as resources) or are produced from boundary conditions as an initially homogeneous system evolves. The important point here is that, whatever their origin, random elements can only be incorporated into a macroscopic description in a statistical sense, and hence cannot be understood in terms of deterministic theories of chemical kinetics or transport.

These general ideas are most easily understood in terms of a specific problem. Consider the transitions discussed previously which might correspond to an explosive pest outbreak. In general a variety of 'hot spots' can occur in such disturbed communities (gamodemes varying in different genetic composition, physiological states and habitat). The occurrence, distribution, and properties of these localized disturbances vary at random throughout the system. Moreover, since interaction of spatially localized 'hot spots' leads to positive feedback on small 'microexplosions,' the space-time distribution of such nuclei for instability should be treated explicitly. A deterministic model, even if it could include the necessary detail, would yield a unique evolution for each possible initial distribution. With a large number number of degrees of freedom in specifying the initial condition, it is essentially impossible in this way to sample the system's state space adequately. This indeterminacy already suggests that statistical ideas are appropriate, an idea advanced for similar reasons in recent reports by Jeffery (1977) and Turner (1978).

Stochastic Theory

To introduce the basic ideas of stochastic theory appropriate to the problem at hand, let us specialize to the case of chemical kinetics. Generalization of the methods in a biological context is straight forward. Consider an open, multicomponent mixture of chemical species S_n ($n = 1, \dots, N$) among which M reactions R_μ ($\mu = 1, \dots, M$) are possible. If $X_n(r, t)$ denotes the concentration of species S_n at position $\underline{r}$ at time t , then the equations of mass balance take the form

$$\frac{\partial X_n(\underline{r}, t)}{\partial t} = F_n(\{X_k(\underline{r}, t)\}) + D_n \nabla^2 X_n(\underline{r}, t) \quad (17)$$

where for convenience only diffusive transport is included. The first term gives the change due to chemical reactions

$$F_n(\{X\}) = \sum_{\mu} \nu_{n\mu} V_\mu$$

with ν_{nm} the stoichiometric coefficient for species S_n in reaction R_m and V_m the rate of reaction R_m .

Stochastic formulations of the reaction-diffusion problem can take many forms. In principle every variable. Variations in X_n reflect molecular fluctuations or initial inhomogeneities, while inhomogeneity or uncertainty in several parameters may lead to variations in the rate constants and transport coefficients. Analytical stochastic theories typically treat one or more types of random elements and lead to descriptions in terms of Markovian master equations, Fokker-Planck equations, or stochastic differential equations. The different theoretical description all have their own domains of applicability, advantages and disadvantages, but all are virtually intractable when more than a few degrees of freedom are involved, and none are easily adapted for numerical solution. Hence practical application of stochastic methods to complex systems demands a new approach, and in particular requires one which can be efficiently implemented using high-speed computers.

Stochastic Simulations of Homogeneous Systems

Stochastic simulations focus on events rather than constituents, and evolution of concentrations (or populations) is followed as a random sequence of events is generated in a statistically consistent simulation. In the language of a Markovian stochastic description (of chemical kinetics), the basic method is expressed in terms of the probability $P(\gamma, \mu) \delta t$ that the next event will occur in the infinitesimal time increment δt following an interval γ and will be an event type μ . Within this framework the transition probabilities for various kinetic processes take the general form

$$W_\mu(t) \delta t = C_\mu k_\mu \delta t \quad (19)$$

Here h_μ is a combinatorial factor expressing the number of distinct ways that the species necessary for an R_μ reaction can be selected from the populations within homogeneous volume V at time t . The quantity $C_\mu \delta t$ is then the average probability that a particular combination of reactant molecules will react species populations, respectively, as one would expect intuitively from macroscopic considerations.

Turning now to the reaction probability function $P(\gamma, \mu)$, we can write an exact expression based on the Markovian stochastic theory

$$P(\gamma, \mu) = h_\mu C_\mu \exp \left\{ -\gamma \sum_{r=1}^M h_r C_r \right\} \quad (20)$$

Depending as it does on the instantaneous values of C_μ and h_μ for all reactions $P(\gamma, \mu)$ is evidently a complicated function of the evolving chemical state of the system. Using this function, however, it is possible to construct a rigorous algorithm for simulation of a stochastic chemical evolution. The algorithm involves a proper random

(Monte Carlo) selection, at a time t , of quantities $\mathcal{T}$ and $\mathcal{M}$ which completely specify the next chemical event which will occur.

This selection process is then iterated, beginning from an initial state of the system, as defined by species populations, to simulate a chemical or biological evolution. A statistical ensemble is generated by repeated simulation of the evolution using different sequences of random number in the Monte Carlo selection process. Within limits imposed by computer-time restrictions, ensemble population averages and relevant statistical information can be evaluated to any desired degree of accuracy.

In recent years several algorithms involving stochastic simulations have been implemented successfully, and applications for a variety of test problems involving relatively simple chemical systems especially, have been carried out (Gillespie, 1976; Turner, 1968, 1977). The success of these bench mark simulations together with the simplicity of the required algorithms (as compared with integrating differential equations), provide strong motivation for developing methods which can treat the spatial heterogeneity characteristic of kinetic systems in physics, chemistry, and biology.

Space Dependence in Grid Form

The simplest method of introducing space dependence is to begin with a uniform spatial grid. Consider a one-dimensional system (for convenience) of length L subdivided into K cells of length $l = L/K$. If M reactions R are possible among N chemical species S_n , then there are $M + 2N$ independent processes which depend on the contents of each individual cell. That is, within each cell, M reactive processes are possible, and these depend only on the N populations X_n within that cell. In addition, there are two independent diffusive processes for every species within cell k , one each to adjacent cells $k - 1$ and $k + 1$. In passing from a global to a local description, therefore, the sample space of independent events has increased from M to $K(M + N)$. The reaction probability density function of Eq. (20) is redefined to include all relevant processes of reaction and diffusion, and the algorithm is developed as in the homogeneous case, with $h_{n\mu}$ for diffusive transport of Species S_n from cell k given by $d_n X_{n,k} (D_n = D_n/l)$.

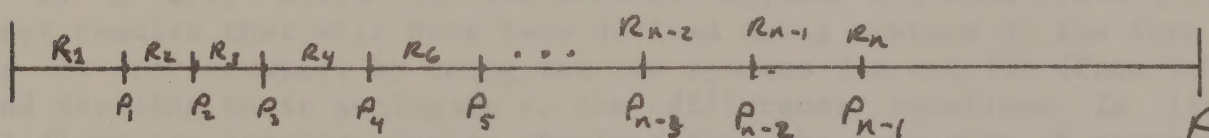
Recently the grid model for space dependence has been extended to two and three space dimensions by one of us (J.S.T.), and has been implemented successfully in several test cases taken from chemical kinetics. These new methods permit studies which are beyond the reach of numerical methods for differential equations even at the deterministic level of description. They will be important in later stages of our studies which will involve incorporating spatial aspects of niche overlap and competition. Problems of spatial localization and nucleation can also be addressed with these new methods of stochastic simulation. In the form discussed here by way of introduction, stochastic simulations of the one-at-a-time type are limited to relatively small number of elements of the various types. Thus populations of order 10^3 to 10^5 are reasonable.

Higher-Level Stochastic Simulations

The methods discussed so far all deal with 'one-event-at-a-time,' and hence constitute the lowest-level stochastic description above the actual microscopic dynamics. Obviously a higher-level algorithm is essential to treat macroscopic systems at the level at which spatial effects enter the system explicitly. Let us now outline briefly the ideas needed for passage to such a higher level:

Instead of considering one event at a time in the whole system (which may be divided into 'cells' in one to three dimensions), one needs to treat the occurrence of N_r events in time τ_r , where N_r and τ_r are large enough that macroscopic systems are feasible. At the highest level, such a description of reaction/diffusion systems involves coupled partial differential equations. This is not the main interest, although it would be important as a benchmark limit. The main idea is to produce a macroscopic description which retains the stochastic elements that govern the evolution of real systems, especially near points of instability. In non-ideal (i.e., 'real') systems, molecular fluctuations are likely much less important near instabilities than are small but 'supermolecular' inhomogeneities in composition, density, temperature, etc. Such 'microscopically large' scale features provide the nuclei for transition transitions to combustion, explosion, or detonation, for example, and render completely ineffective the predictions of deterministic methods.

Again suppose that M reactions R_μ may occur among N species S_N , and consider a homogeneous (i.e., single-cell) system for convenience. The one-at-a-time method constructs a linear probability space divided into slots corresponding to the individual events R_μ which are possible at any instant,



where

$$P_r = \sum_{\mu=1}^M W_{r\mu} \quad \mu=1, \dots, M \quad (W_0 = 0) \quad (21)$$

The simulation procedure discussed so far follows rigorously from the theory of Markov processes. To extend the method to ' N_r events (in time τ_r) at a time,' the obvious approach is to "draw N 'items' (events) from the M slots of the linear probability space," where in general we would like $N_r \gg M$. A consistent interplay between diffusion and reaction will determine the most natural N_r for systems of specified dimension and number of particles. Note that the τ -determination is automatically coupled to the total probability (analogous to 'rate' at the macroscopic

level), so that time-step-control is automatic. This means that no stiff coupling due to kinetic processes, and probably also none due to discretization of space in two and three dimensions.

3.3.2 Objectives -

The general objective of this study is to develop and analyze systems of differential equations that will, under certain methods of analysis, techniques such as computer simulations, local stability analysis and structural stability analysis will show the qualitative conditions under which rapid speciation and the coevolution of community interactions occur. To accomplish this goal however, we must first construct a theoretical basis which integrates ideas from both population ecology and genetics. In order to do this, we must accomplish several specific goals which will be pursued over the next three years of this research:

1. benchmark models in Table 2
2. generalize the models in Table 2 to take into account mutations, fluctuations, and resource dynamics
3. develop models similar to those in Table 3 (which will include genetic variables) to incorporate speciation mechanisms, phyletic species packing, habitat selection, etc.

Objective One. We will analyze the general differential equation models we have derived in Table 2 to determine the assumptions which produce analogous results to those equations in Table 1. Some of these are shown in Table 3, and an example for the case of density-dependent selection is discussed in section 3.2.1.1. Accomplishing this objective will be a step built on the work of Nagylaki and Crow (1974), will connect results that will have been derived using systems of the form in Table 1. For example, by using the two systems IIa and IIb (from Table 2) and deriving their analogues to the difference equations Ia (from Table 1) we can compare results obtained from the same sets of parameter values and numerically integrating them to obtain a phase portrait like Roughgarden's (1971), or analyze them like Anderson's (1971) and Charlesworth's (1971) local stability analysis. Using the parameter values given by Asmussen and Feldman (1977) we determine effects of parameter changes on the dynamics of the system in terms of Lyapunov stability and structural stability. Thus we can compare the two types of systems in terms of the criteria shown in Tables 4 and 5 to verify the predictions as cited from the literature. In addition, we can examine the continuous system to determine how the amount of genetic variance present in the population affects the rate of increase in fitness of the genotype and average fitness of the population. This will enable us to compare how a number of ecological interactions affects the conclusion of FSTNS, and Wright's equation on an adaptive topography (See section 3.1.2). Some related work has recently been reported using a system of the form in Table 1 (Leon and Charlesworth, 1978; Levin, 1978), which give results with which to compare to our own investigations.

Objective Two. After we investigate the dynamics of the general equations of the form in Table 2 we will be able to begin modifications to account for mutations, stochastic fluctuations and resource dynamics. Some possible equations for investigation are in Table 3. As discussed in section 3.2, we build upon a number of results from Allen (1976) and Deneubourg (1976) since these are the few benchmarks that exist in this area. The work done by these investigators in Brussels will help us to formulate the rigorous theoretical basis required to study evolutionary dynamics and will facilitate our understanding of the effects of ecological interactions on speciation mechanisms. This phase of the study will probably take more than the last half of the first year, but will ease the transition into focusing on the major problems of this study, phyletic species packing and its effects on community dynamics and statics.

Objective Three. The third objective of the study is anticipated to occupy the last year and a half of more of research. It involves incorporating speciation mechanisms, types of mating structures and habitat selection into the general models in Tables 2 and 3. This phase of the project most likely will be devoted to simulations to investigate conditions which cause rapid speciation. The results obtained in previous objectives will allow us to determine the parameters which affect system dynamics. We can then construct mathematical models incorporating these evolutionary variables and parameters, and we hope to return to experimental tests and field observations based on the appropriate parameters.

TABLE 1. DIFFERENCE EQUATION MODELS OF THE FORM:

$$\Delta N_i = N_i (W_i - 1)$$

$$\Delta p_i = p_i (W_i - \bar{W}) / \bar{W}$$

N_i = pop. density ALLELE i
 p_i = gene frequency ALLELE i
 W_i = selective value ALLELE i

$W_i(N, P_i)$ SELECTIVE VALUE ALLELE i	$\bar{W}(N, P_i)$ AVERAGE SELECTIVE VALUE
Ia. (4, 7, 24) Density-Dependent Model: $W_i(N) = \sum_j p_{ij}(t) W_{ij}(N)$ $W_{ij}(N) = 1 + \frac{r_{ij}}{K_{ij}} (K_{ij} - N)$ where: r_{ij} = INTRINSIC RATE OF INCREASE genotype A_{ij} K_{ij} = CARRYING capacity genotype A_{ij}	$\bar{W}(N) = \sum_{ij} p_{ij}(t) W_{ij}(N)$
Ib. (13, 25) Competition Model: $W_i^A(N^A) = \sum_j p_j^A(t) W_{ij}^A(N^A)$ $W_i^B(N^B) = \sum_j p_j^B(t) W_{ij}^B(N^B)$ where A, B represent Two competing species	$\bar{W}^A(N) = \sum p_i^A(t) p_j(t) W_{ij}^A(N)$ $\bar{W}^B(N) = \sum p_i^B(t) p_j(t) W_{ij}^B(N)$

TABLE I. (CONTINUED)

$W(N, P_i)$	$W(N, P_i)$
$W_{ij}^A(N) = 1 + R_{ij}^A [K_{ij}^A - N^A(t) - \alpha_{ij} N^B(t)] / K_{ij}^A$ $W_{ij}^B(N) = 1 + R_{ij}^B [K_{ij}^B - N^B(t) - \beta_{ij} N^A(t)] / K_{ij}^B$ where, $R_{ij}^{A,B}, K_{ij}^{A,B}$, defined as above α_{ij} = competition coefficient β_{ij} = competition coefficient	
Ic. (24) Predator-Prey Model: $W_i^1 = \sum_j P_j^1(t) W_{ij}^1(N^1)$ $W_i^2 = \sum_j P_j^2(t) W_{ij}^2(N^2)$ $W_{ij}^1 = 1 + \frac{r_{ij}}{K_{ij}} N^2 - [a_{ij,11} P_2^2 + a_{ij,12} 2 P_2(1-P_2) + a_{ij,22} (1-P_2)^2] N_2$ $W_{ij}^2 = 1 - d_{ij} + [P_1^2 a_{11,ij} + 2 P_1(1-P_1) a_{12,ij} + (1-P_1)^2 a_{22,ij}] N_1$ where, r_{ij}, K_{ij} = defined as above $a_{11,ij}, \dots, a_{22,ij}$ = 'evolution' parameters of ability of prey and predator to survive [genotypes] Predation rate of $A_i A_j$ in the predators against genotype $A_i A_j$ in the prey d_{ij} = death rate predator, i, j the genotype	$\bar{W}^1 = \sum_{ij} P_i^1 P_j^1 W_{ij}^1$ $\bar{W}^2 = \sum_{ij} P_i^2 P_j^2 W_{ij}^2$

TABLE II. DIFFERENTIAL EQUATION MODELS OF THE FORM:

$$\dot{N}_i = \sum_j \dot{n}_{ij} = \sum_j F_{ij}(N, P) \quad ; \quad \dot{N} = \sum_i \dot{n}_{ij}$$

[HERE WE SHOW ONLY $\dot{n}_{ij}$ EXPLICITLY $\dot{P}_{ij}$ 'S CAN BE EASILY FOUND]

$$F_{ij}(N, P_i)$$

IIa. (17, 18)

'SIMPLE' GENETIC MODEL:

$$N \left[\sum_{k \neq j} X_{ik, jk} a_{ik, jk} - d_{ij} P_{ij} \right]$$

where

$$N(t) = \sum_{ij} n_{ij}(t) = \text{TOTAL NUMBER OF INDIVIDUALS}$$

$X_{ik, jk}^{(t)}$ = proportion of MATINGS between genotypes $A_{ij} \times A_{kl}$

$a_{ik, jk}$ = average fertility of $A_{ij} \times A_{kl}$ mating

d_{ij} = Average death rate of A_{ij} genotypes

IIb. (8)

$$n_{ij}(\tau, 0) + \int_0^d n_{ij}(\tau, x) \left[\frac{\partial l_{ij}(\tau, x)}{\partial \tau} + \frac{\partial l_{ij}(\tau, x)}{\partial x} \right] dx$$

$$n_{ij}(\tau, 0) = \iint Y_{ik} Y_{jl}(\tau, x, y) a_{ik, jl}(\tau, x, y) dy dx$$

$l_{ij}(\tau, x)$ = survivorship, ij th genotype A_{ij}

$Y_{ik, jl}(\tau, x, y) \Delta \tau \Delta x \Delta y$ = number of matings from time τ to $\tau + \Delta \tau$ between $A_i A_j$ individuals aged x to $x + \Delta x$ and $A_k A_l$ (from τ to Δy).

$a_{ik, jl}$ = average fertility of $A_{ij} \times A_{kl}$ mating

TABLE II (CONTINUED)

 $F_{ij}(N, P_i)$

MODELS WITH DENSITY AND FREQUENCY DEPENDENT SELECTION:

IIc.

$$N \left[\sum P_{ik} P_{je} (b_{ij,je} - k_{ij,je}^b N) - P_{ij} (d_{ij} + k_{ij}^d N) \right]$$

where: N = TOTAL POPULATION DENSITY P_{ik}, P_{je} = genotype frequencies of $A_{ij} \times A_{ke}$ mating $b_{ik,je}, k_{ik,je}^b$ = birth rate parameters d_{ij}, k_{ij}^d = death rate parameters

IId.

$$x \left\{ \left[\sum P_{ik} P_{je} [b_{ik,je} - k_{ik,je}^b N\alpha - k_{ij,ke}^b x] - P_{ij} (d_{ij} + k_{ij}^d x) \right] \right\}$$

where: x = TOTAL POPULATION DENSITY P_{ik}, P_{je} = genotype frequencies, $A_{ij} \times A_{ke}$ $b_{ik,je}, k_{ik,je}^b$ = birth rate parameters $k_{ik,je}^d, d_{ij}$ = death rate parameters $N\alpha$ = α th resource, saturation parameter

$$\text{IIe (24). } N \left\{ \sum_{je} \left(\sum_{ik} P_{ik} - N^2 \sum C_{ik} X_{ik} \right) \left(N \sum_{je} P_{je} + N \sum C_{ik} X_{je} \sum C_{ik} X_{ik} \right) - e_{ij} X_{je} \right\}$$

where: N = TOTAL POPULATION DENSITY P_{ik}, P_{je} = genotype frequencies C_{ik}, C_{je} = fertility damping parameter X_{ik}, X_{je} = genotype population densities δ_{ij} = birth rate damping parameter e_{ik} = death rate damping parameters

MODELS OF COMPETITION

 $F_{ij}(N, P)$

II e. (23)

$$M \left\{ \sum_{k \neq j} P_{ik} P_{je} (b_{ik,je} - k_{ik,je}^b M) - P_{ij} (d_{ij} + k_{ij}^d M) - P_{ij} \sum_{r \in N} \alpha_{r \in N} \right\}$$

$$N \left\{ \sum_{k \neq j} Q_{ik} Q_{je} (\tilde{b}_{ik,je} - \tilde{k}_{ik,je}^b N) - Q_{ij} (\tilde{d}_{ij} + \tilde{k}_{ij}^d N) - Q_{ij} \sum_{r \in P} \alpha_{r \in P} M \right\}$$

where: N_{ij}, M_{ij} = population densities M and N th species
 $P_{ik}, P_{je}, Q_{ik}, Q_{je} = P_{ij}$ genotype, $Q_{ij} \times Q_{je}$ mating genotypes
 $b_{ik,je}, \tilde{b}_{ik,je}, k_{ik,je}^b, \tilde{k}_{ik,je}^b$ = birth rate parameters
 $b_{ij}, \tilde{b}_{ij}, d_{ij}, \tilde{d}_{ij}$ = death rate parameters

II f.

$$x \left\{ \sum_{k \neq j} P_{ik} P_{je} [(k_{ik,je}^b + k_{ij}^d) N_{ij}^\alpha - k_{ik,je}^b x] - P_{ij} (d_{ij} + k_{ij}^d x) - P_{ij} \sum (k_{ik,je}^b + k_{ik,je}^d) \alpha_{ij} y \right\}$$

$$y \left\{ \sum_{k \neq j} Q_{ik} Q_{je} [(\tilde{k}_{ik,je}^b + \tilde{k}_{ij}^d) N_{ij}^\beta - \tilde{k}_{ik,je}^b y] - Q_{ij} (\tilde{d}_{ij} + \tilde{k}_{ij}^d y) - Q_{ij} \sum (\tilde{k}_{ik,je}^b + \tilde{k}_{ij}^d) \beta_{ij} x \right\}$$

where: x, y = population densities x and x th species
 $P_{ik}, P_{je}, Q_{ik}, Q_{je} =$ genotype frequencies $ij \times kl$ mating
 $b_{ij}, \tilde{b}_{ij}, d_{ij}, \tilde{d}_{ij}$ = death rate parameters
 α_{ij}, β_{ij} = resource utilization parameter / interaction parameters
 N^α, N^β = saturation parameter

TABLE III. MODELS THAT CAN BE DERIVED FROM GENERAL SYSTEMS SHOWN IN TABLE TWO AND RELATED TO MODELS IN TABLE 1.

III a.

$$\dot{N}_{ij} = P_{ij} r_{ij} N (1 - N/k_{ij})$$

$$\dot{P}_{ij} = P_{ij} r_{ij} (1 - N/k_{ij}) - \sum_{ij} P_{ij}^2 r_{ij} (1 - N/k_{ij})$$

VARIABLES AND PARAMETERS defined AS IN TABLE 1.
SEE SECTION 3.2.1.1

III b.

$$\dot{X}_i = k_i X_i \sum_{\alpha} \beta_{\alpha i} (N_{\alpha} - \sum_j \beta_{\alpha j} X_j) - d_i X_i$$

SEE SECTION, 3.2.1.3, CASE I.

III c.

$$\dot{X}_{u,i} = \sum_k k_u^{(u)} X_{u,k} \sum_{\alpha} \beta_{\alpha k}^{(u)} (N_{\alpha} - \sum_{j,v} \beta_{\alpha j}^{(v)} X_{j,v} - d_i X_{u,i})$$

SEE SECTION, 3.2.1.3, CASE III.

III d. (3) COMPETITION Model :

$$\dot{X}_{11} = \frac{k_{11} (X_{11}^2 + \frac{X_{12}}{4} + X_{11} X_{12}) (N_{11} - X_{11} - \alpha X_{12} - \gamma X_{22}) - d_{11} X_{11}}{X_{11} + X_{12} + X_{22}}$$

$$\dot{X}_{12} = \frac{k_{12} (X_{12} X_{11} + X_{12}^2/2 + 2 X_{11} X_{22}) (N_{12} - X_{12} + \beta X_{11} - \gamma X_{22}) - d_{12} X_{12}}{X_{11} + X_{12} + X_{22}}$$

$$\dot{X}_{22} = \frac{k_{22} (X_{12} X_{22} + X_{12}^2/4 + X_{22}^2) (N_{22} - X_{22} - \gamma X_{12} - \gamma X_{11}) - d_{22} X_{22}}{X_{11} + X_{12} + X_{22}}$$

TABLE III (CONTINUED)

where:

x_{ij} = population density of ij th genotype

k_{ij} = birth rate parameter ij th genotype

N_{ij} = saturation parameter ij th genotype

$\alpha, \tau, \beta, \kappa$ = parameters describing competitive interactions

d_{ij} = death rate parameter ij th genotype.

II e.(3) Predator - Prey model:

$$\dot{X}_{AA} = k \left\{ X_{AA}^2/2 + X_{AA}X_{AB}/2 + X_{AB}^2/8 \right\} \left\{ \frac{N}{X} - 1 \right\} - S X_{AA} Y$$

$$\dot{X}_{AB} = k \left\{ X_{AA}^2/4 + X_{AA}X_{AB}/2 + X_{BB}X_{AB}/2 + X_{AA}X_{BB} \right\} \left\{ \frac{N}{X} - 1 \right\} - S X_{AB} Y$$

$$\dot{X}_{BB} = k \left\{ X_{BB}^2/2 + X_{AB}X_{BB}/2 + X_{AB}^2/8 \right\} \left\{ \frac{N}{X} - 1 \right\} - S X_{BB} Y$$

$$\dot{Y} = -dY + (X_{AA} + X_{AB} + X_{BB})SY$$

where:

X_{AA}, X_{AB}, X_{BB} = genotype pop-density of the prey

Y = density of the predator

k = constant expressing the ability of a genotypic couple to find food to maintain themselves, produce offspring.

S = death rate, ability of genotypes to avoid predators, etc.

d = death rate predator

N = saturation parameter

TABLE 4

MODEL:	Ia (4,24)	IIe	IIId (2)	IIc (26)
Interaction	Density Dependence	Frequency and Density Dependence (26)	Frequency, density Dependence (15)	Frequency and Density Dependence (6,9,26)
Genotypes Density Dependent	Yes	Yes	Yes	Yes
Genotypes Intraspecific Frequency Dependent	No (24)	Yes (14,9)	Yes (26,9)	Yes (8,13,26)
Mutations can be Introduced	Yes; structural changes possible?	Yes	Yes; structural changes possible (1,2,3,25)	Yes
Stochastic Fluctuations can be Introduced	Yes, over a restricted range (14)	Yes	Yes, over a wide range of parameters (1,2)	Yes
Resource Dynamics Explicit	No parameters describing resource utilization	No	Explicit parameters for resource use (1,2,3,19,22)	Explicit parameters for resource use
Evolutionary Equilibrium Assumed	Locally stable (24)	No	Dynamic Evol'nry processes drive to non-equilibrium state (1,2,3,19,22)	Yes (1,2,3,9,10,11)
Hardy-Weinberg Equilibrium Assumed	Yes (14,24)	No (17,26)	No (1,2,3)	No (2,26)

TABLE 5

MODEL:	Ib (13)	Id (13,15)	IIg (2)	IIh
Ecological Interaction	Competition	Multispecies Interactions	Competition	Multispecies
Genotypes Density Dependent	Yes (13,14)	Yes (13,14,15)	Yes (2,3)	Yes (2,3)
Genotypes Frequency Dependent	No (13)	No (14)	Yes	Yes
Mutation can be Introduced	Yes, can evaluate only locally (13)	Yes (14)	Yes, evaluate structural stability (2,3,25)	Yes (2,3)
Random Fluctuation can be Introduced	Yes (13)	Yes (14)	Yes (1,2,3)	Yes (2,3)
Resource Dynamics Explicitly Included	No	No	Yes (19,2,3)	Yes, parameters for resource use (2,19)
Species Packing Explicitly Included	Not in stated form	Not in stated form	Yes (3)	Yes
Social Interaction Possible	No	No	Yes (10,11)	Yes (10)
Evolutionary Equilibrium Assumed	Yes, locally stable equilibrium (13)	Yes, locally stable equilibrium (14)	No	No, assume evolution <u>drives</u> system to <u>non-equilibrium</u> state
Hardy-Weinberg Equilibrium	Assumed (13,15)	Assumed (14)	Not assumed (17,26)	Not assumed (1,2,3)
Dynamical Simulations	Tractability low (5,20,21)	Not tractable (5,20,21)	By design (1,2,3,10,11,19)	By design (1,2,3,10)
Mathematical Complexity	Low (14,24)	Low (14,24)	High (21,22)	High (1,2)

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10.0 APPENDIX A: SELECTION FOR ANEMOTAXIS ... (JOHNSTON)

11.0 APPENDIX B: A NEW CACTIPHILIC DROSOPHILA NICHE ... (JOHNSTON)

12.0 APPENDIX C: GENETIC CLUSTER ANALYSIS ... (SMOUSE & RICHARDSON)

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